

The Canadian Entomologist

Vol. LXXXIX

Ottawa, Canada, February 1957

No. 2

The Interpretation of Mortality Data in Studies on Population Dynamics¹

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Introduction

Biologists in general, and entomologists in particular, have published many data of the 'percentage mortality' type. It appears to be a natural tendency in the ecological study of an insect to attempt to measure the degree of mortality caused by different factors. Early publications listed many figures on 'percentage parasitism' because it was one of the easiest mortalities to measure. More recently, as better techniques were developed for population sampling and mortality assessment, it has been possible to derive mortality data for other factors. Notable progress has even been made with such difficult problems as measuring the mortality caused by avian, mammalian, and invertebrate predators. Despite these developments, life tables generally show some residual mortality that cannot be attributed to a specific factor. Frequent population measurement can establish the exact time of such mortality, however, while concomitant work on behaviour, physical ecology, and inherent factors can provide very useful clues as to what intrinsic or extrinsic factors it may be related. Fairly complete life tables are already available for natural populations of a few species, and will no doubt become available for additional species from time to time.

Too often, however, we tend to overlook the fact that these mortality estimates do not represent an ultimate objective in population work. Long columns of percentages, which are sometimes presented only with the conclusion that high percentages indicate important mortality factors and low percentages indicate unimportant ones, contribute little to our understanding of population dynamics. It is only after very careful interpretation that mortality data begin to serve a useful purpose by helping us to understand the fascinating problem of animal numbers. Perhaps a major reason for this frequent lack of complete analysis is the confusion and misunderstanding that exist concerning the proper interpretation of mortality data. There are nearly as many different ideas in the literature as there are papers on the subject. In the present paper it is proposed to review these ideas, to examine them in conjunction with some life table data for the spruce budworm, *Choristoneura fumiferana* (Clem.), and to attempt to reach some conclusions concerning the interpretation of mortality in natural populations.

'Mortality' will be used here in a broad sense to cover any loss in a given population, whether this loss results from direct mortality, from dispersal, or from reduced fecundity. Morris and Miller (1954) have shown that it is convenient to tabulate all these losses in one ' d_x ' column in the development of life tables. Other authors (Voûte, 1943) have proposed the use of "R-factors" (where R=Resistance or Reduction) to satisfy the fact that such losses as reduced fecundity do not constitute a direct mortality of individuals. As this expression has not yet found its way into North American literature, the more familiar term 'mortality' is retained here.

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Review of Ideas

This chronological review will be as brief as is consistent with a desire to use the authors' own words wherever possible. Discussion of the ideas will come under later headings.

Howard and Fiske (1911, p. 116) observed that "A 50 per cent parasitism of the eggs followed by another 50 per cent parasitism of the caterpillars, could not by any possibility be considered as resulting in 100 per cent parasitism or complete extinction, but only in 50 per cent parasitism added to 50 per cent of what remained, which amounted, in effect, to 25 per cent of the whole. In this manner an aggregate of 75 per cent only is secured". This observation was the point of departure for the work of Thompson and others on the interpretation of the effects of mortality factors acting in sequence.

Thompson (1928) distinguished between "apparent" and "real" mortality: "Let us suppose that we have an insect population of one hundred larvae per unit area and that the adult female of the species considered deposits one hundred eggs, giving fifty males and fifty females. In that case a destruction of 98 per cent of the larvae per generation, so as to leave one female and one male would correspond to a position of equilibrium, or in other words to a population constant from generation to generation. Let us suppose that the 98 per cent destruction of the population is accomplished by a series of parasitic and other factors acting successively, the proportional destruction of the population actually present in each of these successive stages being a, b, c, d, \dots etc. A collection of eggs made at the beginning of the life cycle will then show that the fraction a is destroyed by the first factor; a collection of eggs and larvae made from the population remaining after the first factor had operated (including, of course, none of the individuals killed by this factor) will show that the fraction b is destroyed by the second factor; a collection made after this factor has taken effect and including no individuals killed by it would show the fraction c in process of destruction by a third factor, and so on. The total fraction of the population present at the beginning of the life cycle, destroyed by all the factors taken together can then be represented by the equation

$D = 0.98 = a + (1-a)b + (1-a)(1-b)c + (1-a)(1-b)(1-c)d + \dots$ to x terms, where there are x factors involved.

". . . . If we represent by the symbols A, B, C and D the fractions of the total initial population destroyed by each of the factors F1, F2, F3, F4, etc., considered, the value of A, B, C and D will of course be as follows:

$$\begin{aligned} A &= a \\ B &= (1-a)b \\ C &= (1-a)(1-b)c \\ D &= (1-a)(1-b)(1-c)d \end{aligned}$$

"Calling A, B, C, D, etc. the *real* destruction and a, b, c, d , etc., the *apparent* destruction, the difference between the two will be evident from the following table:

Factor	App. destr.	Real destr.
F1	a	a
F2	b	$(1-a)b$
F3	c	$(1-a)(1-b)c$
F4	d	$(1-a)(1-b)(1-c)d$

A number of numerical examples are listed, including the following:

Factor	App. destr.	Real destr.
F1	0.5 or 50%	0.5 or 50%
F2	0.5 or 50%	0.25 or 25%
F3	0.5 or 50%	0.125 or 12.5%
F4	0.5 or 50%	0.0625 or 6.25%
Total		0.9375 or 93.75%

These examples show that the difference between real and apparent mortality may be enormous, and Thompson stresses the importance of real mortality in indicating the controlling value of a given factor. He further concludes, "The real significance of a controlling factor depends, however, not merely upon the fraction of the total host population it actually destroys, but rather upon the fraction of the population for the destruction of which it is indispensable". To find this latter fraction he uses the basic formula quoted above and calculates the effect on total generation mortality when one or more of the mortality factors disappears from the complex. Thus the "indispensable" mortality, a term which Thompson (1955) later changes to "irreplaceable" mortality, is that part of the total generation mortality which could not occur in the absence of a certain factor, despite the action of subsequent factors. When factors disappear from a complex of "general" factors (those whose proportional effect on population is independent of population density) the effect on generation mortality is a minimum; "since the apparent mortality remains constant, the factors which disappear are to a large extent automatically replaced by those which follow them". But when factors disappear from a complex of "individualised" factors (those whose proportional effect, or apparent mortality, depends in some way on the numerical value of the host population) the effect is a maximum, since those that remain cannot replace the effect of those that have disappeared. From his final example (pp. 104, 105), which includes factors of both types, he considers the effect produced by removing the individualised or density-related factor (parasites) from a complex of general factors:

"Thus the absence of parasites causing a 10.0 per cent apparent mortality in the egg stage, a 60.0 per cent apparent mortality in the larval stage and a 10.0 per cent mortality in the pupal stage, i.e., an 80 per cent total apparent mortality, would have a much less disastrous effect than might be supposed. The total destruction would fall only 4.0 per cent. The absence of the parasites would allow the escape for reproduction of only two additional females per hundred. Since such an enormous fluctuation in the apparent mortality has so little effect, it is evident that slight fluctuations will ordinarily be of no importance".

Nicholson (1933) concluded, in a passage that has been very frequently quoted by other workers, "If an attempt is made to assess the relative importance of the various factors known to influence a population, no reliance whatever must be placed upon the proportion of animals destroyed by each. Instead, we must find which of the factors are influenced, and how readily they are influenced, by changes in the density of animals". Smith (1935) expressed a similar point of view.

Bodenheimer (1938, p. 105) stated that "All factors are of destructive value in direct proportion to the percentage per stage destroyed by each". In other words, a mortality factor that kills 50% of one stage of an insect is five times as effective as a factor that kills 10% of the same stage. This is about the simplest possible interpretation of mortality data and seems to have been accepted, at least implicitly, by many entomologists.

Balch and Bird (1944) presented an interpretation of field mortality data for

the European spruce sawfly, *Diprion hercyniae* (Htg.), with the object of showing the role of a virus disease in its natural control. Their analysis was complicated by the occurrence of two overlapping generations per year, and the following description will be somewhat oversimplified in the interests of brevity. They reasoned, as had Thompson, that the effectiveness of a mortality factor would best be revealed by its influence on the total mortality per generation. To show the effects of generation mortality on the course of events they introduced the term "Index of population trend", which was simply $I = 100$ (population in one year/population in preceding year). The use of this Index revealed the importance of very small changes in generation mortality. A generation mortality of slightly over 97% was necessary to maintain a level sawfly population ($I = 100$). Before the disease appeared other factors were giving a generation mortality of 95% on some plots, but this permitted a geometric increase of more than 2-fold per year ($I = 200$ plus). The disease increased generation mortality to over 99% ($I = 20$, roughly) and brought about a drastic decline in population over a period of a few years. Although the importance of small changes at high levels of mortality was clearly shown by the data, it was not elaborated by the authors beyond the following sentence: "Percentages are shown to the first decimal point regardless of the significance of the data, to demonstrate the importance of fractional changes in such percentages as they approach 100".

Bess (1945) devised "mortality/survival ratios" (M/S) for the interpretation of percentage mortality data. "The insects that escape death from the mortality factors are the ones that are important from the standpoint of potential increase. . . . Examples will be given first to illustrate that percentages of mortality do not clearly show the relative influence of different degrees of mortality in reducing the number of survivors, or the survival population.

"Let it be assumed that tests have been made with certain insecticides and the following information obtained when 1,000 insects were used in each test: Insecticide A killed 50 per cent, or 500 insects; insecticide B killed 90 per cent, or 900 insects; insecticide A plus a third material, C, killed 55 per cent, or 550 insects, and insecticide B plus a fourth material, D, killed 95 per cent, or 950 insects. Both materials C and D increased the kill 5 per cent, or 50 insects each, but the addition of C reduced the survival population from insecticide A alone only one-tenth, whereas the addition of D reduced the survival population from insecticide B alone by one-half. Therefore, in terms of the survival populations, or the insects left to cause damage, the addition of D was relatively more effective than the addition of C, even though each increased the mortality by 5 per cent, or killed 50 additional insects.

". . . . These data show that small increases in percentage kill are relatively important when high percentages of mortality are involved and that they are of negligible importance at low percentages of mortality. . . . This means that in terms of the survival population at 1 per cent increase in kill at the 95 per cent level would have a greater relative effect on the survival population than a 1 per cent increase in kill at the 50 per cent level. In other words, percentages of mortality have cumulative values, and are therefore of unequal value, if viewed in the light of the survival population, which is the potentially important population.

"If the number or percentage of the insects killed in any stage, or at any time, is divided by the number or percentage of the insects that escaped death, the number thus obtained represents the relative reduction in the survival population

produced by the mortality. This ratio indicates the reduction per individual survivor and the effect of the reduction on the survival population in practically the same way that the per cent increase indicates the relative effect of a certain treatment on the yield of the same crop. For example, if the mortality/survival ratio were multiplied by 100 and expressed as a percentage, it would represent the per cent increase in the survival population which was prevented by the mortality."

Bess presents a number of examples, of which the following excerpt from his Table II will serve to show the general method:

Stage	Population	Per cent mortality	Per cent survival	M/S ratio	Numerical reduction in the adult population attributable to each mortality
Egg.....	100,000	60	40	1.50	192
1st larval.....	40,000	20	80	0.25	32
2nd larval.....	32,000	80	20	4.00	512
3rd larval.....	6,400	95	5	19.00	2,432
Pupal.....	320	60	40	1.50	192
Adult.....	128				

The last column is obtained by multiplying each M/S ratio by the surviving population of 128 adults.

Bess then goes on to show how M/S ratios may be combined, either for one factor (such as parasites) operating through successive stages, or for different factors operating simultaneously through various stages. Two important assumptions are involved: first, that all factors are of the independent type (i.e., not related to host density) and second, that parasites attack their hosts indiscriminately, whether they already contain another parasite or not. They will be discussed in a later section. Like Thompson (1928) and Balch and Bird (1944), Bess bases his conclusions largely on total generation effects and on the concept of indispensable mortality. He considers that the M/S ratio for a given factor is proportional to the effect that would be produced on generation survival by the complete disappearance of the factor from the complex.

Varley (1947) disagreed with Bodenheimer's interpretation of mortality data, pointing out that it applies only to the immediate effects in a single generation. He agreed with Nicholson's interpretation and, using field data for *Urophora jaceana* (Hering), presented an illustration of how the formulae of Nicholson and Bailey (1935) could be applied to life table data. His work showed that it is necessary to develop life tables for both the host and its parasites in order to test the different theories on the action of parasites, and to have actual population data for successive points in the life cycle of the host in addition to percentage mortality data.

Morris and Miller (1954) suggested the adoption of life tables, as used conventionally for human populations, for the analysis of insect mortality data. In these tables, x = age interval, I_x = population at the beginning of x , d_x =

number dying as a result of each mortality factor during x , and $100q_x = d_x$ as a percentage of I_x (i.e., apparent mortality). They emphasized that I_x and d_x should represent actual numbers, based on an absolute sampling unit (Morris, 1955) rather than on some arbitrary scale. Miller (1955) showed the application of this treatment to insect parasites and mentioned, in the same paper, the apparent difference in viewpoint between Thompson (1928) and Bess (1945).

Thompson (1955) believed that Miller was confused and went on to review in some detail his (Thompson's) ideas of 1928 in conjunction with the ideas of Bess. He disagreed with the assumptions made by Bess but showed that the algebraic formulae presented in the 1928 paper could be used in calculating and combining mortality/survival ratios. From this he concluded that no basic disagreement existed, but only differences of appreciation or viewpoint with regard to the same fundamental facts. The tendency in his earlier paper to minimize the significance of small changes in total generation mortality was attributed to the fact that he was thinking in terms of economic damage in the next generation of the insect rather than population trend over a longer period.

Different ideas have been expressed by other authors but as they had more restricted objectives they will not be reviewed here. Most of them concern the problem of interpreting the mortality caused by applied factors, particularly insecticides. Morris and Miller (1954) pointed out that most of the published data on chemical control are conventionally based on survival population and cannot be compared directly with data on natural factors, which are nearly always expressed in terms of the percentage of insects affected. Several investigators have suggested that the change in absolute population would be the best index of the effectiveness of a chemical treatment, and Solomon (1955) has carried this line of reasoning to its logical conclusion:

"Percentage mortality by itself is not a good measure of the practical value of an insecticidal treatment. In a relatively simple case, such as the fumigation of stored products, the control value can be expressed in terms of the time required for the reduced population to return to its former level of density, provided the mode of increase of the population is known.

"Assuming that increase is at a regular exponential rate, the control values of different mortality percentages can be compared in terms of the calculated recovery times; thus, each of the values in the series 99.6, 93.75, 75, 50 and 29 per cent mortality is twice as good as the one that follows it. Such relationships can be deduced from the graph provided, which is essentially a curve of constant exponential growth, made linear by the use of the logarithmic scale".

It is not possible to classify the ideas that have been reviewed in any way that is simple and at the same time accurate. If we are willing to err on the side of simplicity, then different authors have suggested that the importance of a mortality factor is revealed:

- A. By apparent mortality, and varies in direct proportion to apparent mortality.
- B. By indispensable mortality (i.e., the change in total percentage mortality or survival per generation if the factor is removed).
 - (1) And that the change resulting from the disappearance of a factor is likely to have a small influence on the progress of events, especially if the remaining factors are independent of host density.
 - or (2) And that the change resulting from the disappearance of a factor may have a very great influence on the progress of events because

this change is not directly proportional to apparent mortality but is more rapid at high levels of apparent mortality.

- C. Not by the magnitude of apparent or indispensable mortality but only by the relation between mortality and the population density of the insect.

Natural Control and Population Dynamics

It has been somewhat misleading, of course, to quote the above passages out of context because different authors had different objectives in mind. This influenced their interpretation of mortality data and explains, to some extent at least, the differences in opinion. It is incumbent upon the present writer, therefore, to explain what objectives or purposes he has in mind when discussing mortality data.

Natural control is defined by Solomon (1949) to mean "that regulation of the numbers of a natural population which keeps them within the limits of a more or less clearly definable though often very wide range of abundance". This seems to be the sense in which the term is most often used, especially by those who have been primarily concerned with the theoretical aspects of the subject. If this definition is accepted, then the study of natural control alone cannot satisfy all the requirements of the worker who is concerned with an economically important insect. The spruce budworm, for example, is controlled during outbreaks by the depletion of suitable foliage. This keeps its numbers within a definable upper limit, or in other words, prevents them from reaching infinity. For the sake of argument let us say that the decline or suppression of a budworm population after an outbreak is eventually halted by the growth of a new food supply and by the "competition" among natural enemies in searching for a scarce budworm supply. This keeps the population from decreasing to zero. Therefore, since we understand both the upper limitation and the lower conservation of its numbers, we understand the natural control of the insect. This knowledge will be of scant comfort to the forester, however, who needs to understand the why, when, and where of outbreaks so that he may take steps to prevent them or at least to reduce the damage. It is important to know why outbreaks develop and gain momentum in some forest types and not in others, what determines budworm numbers during the long periods between outbreaks, and what permits the release of low populations and thus determines the timing of outbreaks (Wellington, 1952).

Population dynamics is a more recent term which is commonly used to include both the measurement of population changes from generation to generation and the study of the factors responsible for the changes. It is therefore a broader field than the study of natural control. Further, if population dynamics is studied over a sufficient period of years it should show why fluctuations have upper and lower limits. This will lead to an understanding of natural control while providing, at the same time, the other essential information.

The different objectives implied by these two terms have been the basis of much misunderstanding in the field of population research. Nicholson, for example, was mainly concerned with natural control. He reasoned that only density-related mortality factors possess the necessary properties to limit population changes, and hence his interpretation of mortality as quoted above. The student of population dynamics, however, is as interested in the changes in the "steady density" itself as in the changes about the steady density; and, as Solomon (1949) has already pointed out, there may be great practical difficulty in distinguishing the two types of changes in natural populations.

The present writer is concerned with population dynamics and will deal with mortality data from that point of view. In other words—how can mortality data best be interpreted in order to explain changes in population from year to year and from place to place? This objective is clearly different from the one held by some of the authors whose papers have been reviewed. However, this is immaterial for my object is not to criticize these useful contributions to the development of our thinking on natural mortality, but only to show wherein they are inadequate for the general purposes of population dynamics.

The Variation in Mortality

To be able to interpret mortality with respect to its influence on population dynamics, we must first answer a number of basic questions: What is the significance of variation in the degree of mortality and what causes it? Is the general level of mortality significant and are high mortalities necessarily any more important than low ones? Is the order of mortality in relation to preceding or following mortalities of any significance and how is this affected by contemporaneous mortalities? And, finally, how should we express mortality data to permit the best interpretation?

An attempt will be made to answer these questions in the following sections. Table I is presented only to illustrate some of the points that will be made. In a general way, it is based on actual life tables for the spruce budworm as developed over the past ten years for different forest stands on the Green River Watershed in northern New Brunswick. However, a 'mean' life table has little real significance and, furthermore, the present one has been so abbreviated and simplified as to be misleading in some respects (c.f. Morris and Miller, 1954). This is immaterial to the discussion, which is concerned with general principles rather than the population dynamics of the spruce budworm. In Table I the sex ratio

TABLE I

Abbreviated 'Mean' Life Table for Spruce Budworm at Green River, and the Range in Percentage Mortality Observed during the Past 10 Years

Age interval (x)	No. alive at beginning of x (1 _x)	Factors responsible for d _x (d _x F)	No. dying during x (d _x)	d _x as % of 1 _x (100q _x)	Observed range in 100q _x
Egg	200	Parasites	10	5	1-50
		Other	20	10	Small
		Total	30	15	10-60
L ₁₋₂	170	Dispersal	136	80	60-95
L ₃₋₆	34	Parasites	13.6	40	5-60
		Disease	6.8	20	Small
		Other	10.2	30	5-60
		Total	30.6	90	30-98
Pupa	3.4	Parasites	0.3+	10	Small
		Other	0.5+	15	Small
		Total	0.9	25	Small
Moth	2.5	Misc.	0.5	20	?

Generation survival = 2 or 1%
 Generation mortality = 98 or 99%
 Index of population trend = 100

of the budworm has been taken as 50:50 and the mean fecundity as 200 eggs, which is used in place of actual population for the initial I_x . A survival of 2 moths therefore requires a total generation mortality of 99% and provides for a constant population from generation to generation. The observed range in percentage mortality is listed for a few factors that show a wide range and are therefore useful for illustrative purposes.

By variation in mortality I refer to the significant changes that occur from generation to generation or from stand to stand, not the minor variations that are associated with sampling errors. The first point to be established is that it is in this variation in mortality rather than the absolute level of mortality that is the important thing in population dynamics. This point is obvious, of course, for we would not have dynamic populations unless mortality (in the broad sense defined above) was variable. For example, there is a mortality of 10% affecting the eggs of the spruce budworm which may be attributed to such things as infertility and hatching failure. Its variation with place or time during our studies has been slight. It has therefore had no appreciable influence on population changes. We could, in fact, leave it out of life tables and say that the mean fecundity is 180 instead of 200. The same argument would apply if the degree of mortality were 90% instead of 10%; as long as it does not vary it does not contribute to the changes in population, but only to the potential rate of increase or decrease of the species.

For this reason a single life table applying to one generation of an insect, no matter how complete and accurate it may be, reveals little about the population dynamics of the insect. Nor can it be used to indicate the relative importance of the different mortality factors because some of the highest mortalities may be relatively constant while some of the low ones may vary widely.

This interpretation of mortality data leads naturally to a classification of mortality according to whether it is variable or relatively constant. If it is variable, then the next problem is to find what causes variability. To what intrinsic factors of the insect itself or what extrinsic factors of the environment is it related? In an analysis of possible relationships it is helpful to keep in mind all the different theories on natural control so that no possibilities will be overlooked.

Variation may be related to place. The dispersal loss of small larvae varies from 60% to 95% (Table I) and this variation is mainly determined by stand factors, such as the density of host trees and the continuity of the stand. This may help to explain why outbreaks develop in certain types of forest. Within a given stand this mortality is much less variable and probably plays a minor role in population changes, at least until tree mortality caused by severe defoliation reduces the density of the stand. Table I has not been complicated by the inclusion of moth dispersal, which also varies widely in relation to place, foliage depletion, and weather (Morris *et al.*, in press). This attention to mortality variations in place is essential to an understanding of where outbreaks occur, and to the testing of the theories of Thompson (1939) on the role of dispersal in natural control and Voûte (1946) on the importance of faunistic impoverishment in pure stands. "Place" as used here is not necessarily a whole stand. The same approach can be used, for example, to show why barkbeetle populations are related to the physiological condition of individual trees, or why budworm populations are highest on flowering balsam trees.

The importance of mortality variations that are related to population density has already been stressed by Nicholson and others, and Varley has pointed out

that this relationship is of a "delayed" type. The best example in Table I is the variable mortality caused by larval parasites. The depletion of foliage associated with over-population during outbreaks also gives rise to density relationships, including direct starvation, reduced fecundity, and increased dispersal losses. It is not sufficient to assume that all parasites or other biotic factors are density related while physical factors are not. The parasitism of budworm eggs has varied between 1% and 50% but his has not been clearly related to the density of budworm eggs, probably because of the influence of alternate hosts. Nor has the incidence of disease shown any relation to host density to date. Further, larval parasites have reacted to larval density only up to a certain limit. Controlling factors are not revealed by the simple detection of a relationship to population density. Adequate data on the population limits between which the relationship is effective are required.

The importance of climatic relationships is also well known. Direct mortality caused by extreme weather is easy to measure. The indirect and often delayed effects of unfavourable but sub-lethal conditions (Salt, 1955) are more difficult. However, an adequate series of life tables coupled with careful weather records of the right kind should serve to detect any important relationships of this nature. For example, variations in larval mortality (Table I) and in fecundity have been analysed in conjunction with the rate of development and the weather (Greenbank, 1956).

Again, variations in mortality may be related to the intrinsic vigour of the insect and this, in turn, to the "age" of the population (Franz, 1949). To detect such relations we need to know not only the population level but the history of the outbreak, for the same population level may be reached by rising and declining populations. In regard to intrinsic factors, it should be recalled that 'mortality' is being used here in a wide sense to include reductions in fecundity and changes in sex ratio.

The possibility must also be kept in mind that population changes over a period of years may be the result of random variations in mortality (Cole, 1954). This does not necessarily mean that the variations in the different mortalities must each be random in the sense that they are not related to any intrinsic or extrinsic factors, but only that their net result (total generation mortality) may cause population increases in some years and decreases in others in a random sequence, owing to the multiplicity of factors involved. This will be a difficult hypothesis to test and will probably call for the elimination of the other possibilities.

Other factors to which mortality may be related will no doubt occur to the reader, as well as the possibility, so often neglected by population theorists, that one relationship may determine the numbers of a given species for a period of years or at certain levels of population, while quite another relationship may be predominant in other circumstances.

The viewpoint expressed in this section is in agreement with that of Nicholson, at least to the extent that it is the variation in mortality that is important rather than the magnitude. His conclusion that only the density-related variation is important, however, cannot be adopted in a general study of population dynamics because changes in animal populations from place to place or from year to year can result from other relationships.

The viewpoint expressed here is not in agreement with the concept of indispensable mortality for the interpretation of natural mortality data. Although it may seem quite logical to rate the importance of each factor according to the

effect that might be produced by its disappearance, this approach is not very realistic unless there is a good chance that the factor will actually disappear. Natural mortality factors may produce either a relatively constant mortality or a mortality that varies within certain limits, but they seldom disappear from the complex. Larval dispersal of the spruce budworm, for example, gives a high rate of mortality (Table I), especially in open or isolated stands. The calculation of its indispensable component, either by means of real mortality or M/S ratios, would lead to the conclusion that it is a very important factor. Since it is relatively constant in a given situation, however, and not likely to disappear, its contribution to changes in population over a limited period of years in one stand is rather slight.

The limitation of indispensable mortality is shown in the final example presented by Bess (1945, p. 479-80). Parasites, predators, and disease acting in one generation of an insect have respective mortality/survival ratios of (roughly) 7, 34, and 12. From this it is concluded, "These mortality/survival ratios for the different factors indicate that the relative effect of the predators in the above example was over four times that of the parasites and nearly three times that of the diseases, which answers the question as to the relative effectiveness of the different factors in reducing the adult population". This conclusion, of course, may be true for *this one generation* and suggests what might happen if one of these factors were to disappear. If in succeeding generations the effect of predators and disease remains constant, however, the M/S ratios will remain high even though these two factors are playing no part in population changes. At the same time parasites, causing a low but variable mortality, may be directly responsible for population variation. Whether we are dealing with apparent mortalities, real mortalities, or mortality/survival ratios, it is not the magnitude but the variation that is important in population dynamics.

The concept of indispensable mortality may be useful for special problems like the introduction of parasites (which was the subject of Thompson's 1928 paper) or the application of insecticides. These problems concern the removal of factors from a complex or the addition of new factors, largely through man's intervention. Even in these situations, however, the calculation of indispensable mortality in advance must be recognized as somewhat mythical. The addition or removal of a factor may affect the degree of mortality caused by other factors, especially where complex density relationships are involved. "In fact, all we can reasonably hope is that formulations such as those discussed here may provide convenient patterns of thought, serving for the provisional integration of data and indicating lines of research" (Thompson, 1955).

In the remaining sections of the present paper it is proposed to examine the effects on population trend of normal variations in natural mortality, according to the level at which they vary or the order in which they occur. The index of population trend suggested by Balch and Bird will be used to assess the importance of such variations to population dynamics, and no *a priori* assumptions will be made concerning density relationships. This approach differs from that of Thompson in that he used the concept of indispensable mortality as the main criterion and did not translate changes in generation mortality into their relative influences on population trend. It differs from the approach of Bess in that he also used indispensable mortality and, by the application of mortality/survival ratios to individual mortality factors, assumed that all factors are density independent in their action.

The Level of Mortality

If it is accepted that variation in mortality is the important thing and that high mortalities are therefore not necessarily more important than low ones, the next question is this: Is variation at high levels of mortality more important in its effects on population trend than equal variation at low levels of mortality?

Before this question can be answered it is necessary to consider the significance of generation mortality. Most of the authors reviewed above have accepted generation mortality or survival as the criterion for the interpretation of the mortalities that occur successively throughout the life cycle. This is logical for it is this total generation mortality or survival that tells us whether the events within the generation provide for an increase or decrease in population. In Table I there are two survivors (one male and one female) and the fecundity is 200, so the generation mortality of 99% provides for a constant population from generation to generation. If mortality were less than 99% population would increase at the following rate per generation: 2 X at 98%, 3 X at 97%, 4 X at 96%, 5 X at 95%, and so on. If generation mortality were greater than 99% population would decrease at the following rate: 0.9 X at 99.1%, 0.8 X at 99.2%, 0.7 X at 99.3%, 0.6 X at 99.4%, 0.5 X at 99.5%, and so on. Thus, small variations in generation mortality can be very important in population dynamics. Changes in animal populations are geometric and we should not make the mistake of trying to interpret them on an interval or arithmetic scale.

The range of variation in generation mortality is usually small. In some seventy life tables prepared for the spruce budworm to date, covering a rapid increase from low to outbreak population and subsequent suppression resulting from foliage depletion, the range in generation mortality is approximately 95% to 99.8%. At 95% (5-fold geometric increase) the budworm can increase in five years from an endemic level to a level that causes conspicuous defoliation. Schwerdtfeger (1935) has published records of changes in four important defoliators in Germany over a period of 60 years. Varley (1949) reviewed Schwerdtfeger's data and calculated that the net rate of increase, when increase was rapid during the development of outbreaks, was threefold to sevenfold per generation. This supports the conclusion that the natural variation in generation mortality is usually small, at least for many forest defoliators, and that a small deviation can be extremely important if it is maintained for a few years. Thus, from the point of view of population dynamics, we cannot agree with Thompson when he refers to a change of "only" 4% in generation mortality (above). Although this does not give an outbreak population in the next generation, it represents nearly a maximum variation in generation mortality for an insect like the spruce budworm and can lead to very serious consequences if maintained for a few generations.

Biologists now seem to be agreed that there is no relation between the numbers of eggs laid by animals and the abundance of the animals in nature. The measurement of fecundity, therefore, does not indicate the probable rate of population change for the species. The "innate capacity for increase" or "intrinsic rate of natural increase", as reviewed by Andrewartha and Birch (1954), has been used by some workers to provide a more appropriate index than fecundity. It is defined approximately as "the maximal rate of increase attained at any particular combination of temperature, moisture, quality of food, and so on, when the quantity of food, space, and other animals of the same kind are kept at an optimum and other organisms of different kinds are excluded from the experiment". This rate of increase is conventionally determined in the laboratory where the physical environment can be controlled. As a matter of interest,

however, we can base a rough calculation on natural life table data for the spruce budworm by eliminating parasites, predators, disease, and overcrowding, and taking the minimum values that have been recorded for other factors on the assumption that these minima will represent intrinsic mortality under the most favourable field conditions. By this method the innate capacity for increase of the spruce budworm is roughly thirtyfold per generation, far less than would be expected from its fecundity but far greater than any increase that has actually been recorded in the field. The concept is not without value, however, in the interpretation of generation mortality. If we accept this tentative calculation for the budworm, it indicates that generation mortality could never be less than 70%, even if all enemies were absent and physical conditions were very favourable.

In order to ensure that the significance of variation in generation mortality is correctly interpreted, it is advisable to transform generation survival to the ratio of population increase or decrease between two successive generations. The index of population trend suggested by Balch and Bird, which is simply the ratio of increase or decrease multiplied by 100 to eliminate the decimal point, is useful for this purpose. For the data in Table I, where 2 survivors result from an initial population of 2 moths, this index is $I=100(2/2)$ or, more simply, $100(1/1)=100$, which represents a constant population. If generation mortality changes from 70% in one generation to 71% in the next, $I=100(29/30)=97$, approximately, which does not indicate much of a change in population from the level trend represented by $I=100$. However, if generation mortality changes from 95% to 96%, $I=80$; and if it changes from 98% to 99%, $I=50$ and indicates that population has dropped to one-half its former level. In other words, a change of 1% in generation mortality has a small or a large effect on population trend, depending upon the level of mortality at which it occurs.

To illustrate with a more general case, let M_1 represent generation mortality in one generation and M_2 generation mortality in the following generation. By definition, $I=100[(100-M_2)/(100-M_1)]$. If M_2 is 1% higher than M_1 , as in the preceding examples, then $M_2=M_1+1$ and $I=100[(99-M_1)/(100-M_1)]$. This equation represents a rectangular hyperbola, which has been plotted in the upper part of Figure 1, and shows clearly that variations in generation mortality have relatively little effect on population trend (I) until generation mortality reaches the level of about 80%. Above this level changes in generation mortality have a rapidly increasing effect on population trend because the hyperbola is asymptotic to the line $M=99$. A similar hyperbola can readily be drawn for successive decreases of 1% in generation mortality. This will fall above the line $I=100$ but will lead to the same conclusions.

The fact that the importance of mortality variation depends upon the level of mortality is a very important point that was first demonstrated clearly by Bess. Bess pointed out that the variation in survival provides a better index of population changes than does the variation in mortality, and that the effects are proportional to the corresponding mortality/survival ratios. Although he applied this method to the mortality caused by individual factors, we are concerned so far in the present discussion only with total generation mortality and survival. We can illustrate the principle involved, however, by plotting the mortality/survival ratio for the generation (M/S) over generation mortality (M) where, by definition, $M/S=M/(100-M)$. The resulting hyperbola (lower curve in Figure 1) confirms the conclusions that we have already reached by plotting I , the index of population trend.

Now that the significance of variations in generation mortality has been

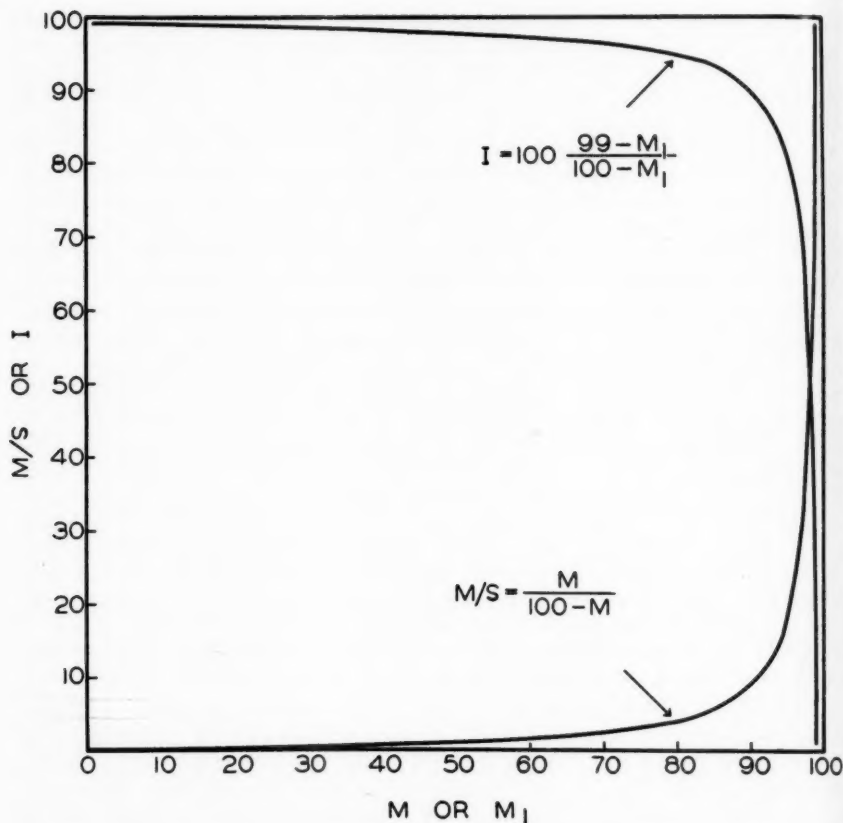


Fig. 1. Lower curve: Mortality/survival ratio (M/S) plotted over percentage mortality (M). The vertical scale has arbitrarily been terminated at M/S=100. Upper curve: Index of population trend (I) when there are successive increases of 1% in generation mortality, plotted over generation mortality (M₁). See text.

brought out, we are in a better position to consider the effects of variations in individual mortalities and to answer the question posed at the beginning of this section. The problem at once becomes more difficult and cannot be solved in any general way unless we are willing to make assumptions of such a simplifying nature that they fail to represent real situations. This difficulty arises from the fact that some mortalities are independent of population density while others are not, as Thompson has already pointed out.

First, let us make the simple assumption that all factors are independent of population density. By simple arithmetic calculations, following Thompson's basic formula for mortalities acting in sequence (above), we can examine the effect on population trend of variations in the different mortalities in Table I. If total egg mortality, which averages 15%, decreases to 5% and all other apparent mortalities remain the same (as they must according to our assumption of density independence), generation mortality is reduced from 99% to approximately

98.9% and $I=100(1.1/1)=110$. Similarly, if the dispersal loss of 80% is reduced to 70%, generation mortality=98.5% and $I=150$; and if the larval mortality of 90% is reduced to 80%, generation mortality=98% and $I=200$. The changes in population trend caused by these three equal variations of 10% in apparent mortality are respectively 10%, 50% and 100%, the differences being dependent upon the levels of mortality at which the variation occurred. These differences are independent of the order of each factor in the sequence, as will be shown in a following section. That is, if we interchange the low egg mortality of 15% and the high larval mortality of 90%, the effect of equal variations still depends solely on the level of mortality at which they occur. According to the assumption of density independence, therefore, variations in apparent mortality become increasingly important to population dynamics when they are associated with factors that normally give a high level of mortality. It is not difficult to show that the relationship is hyperbolic, as already plotted for generation mortality. The treatment of mortality data by Bess was based entirely on the assumption of density independence. If this assumption is true, the change in generation survival attributable to each mortality factor is proportional to the mortality/survival ratio for the factor and we are justified in using M/S ratios (as plotted for generation mortality in Figure 1) in interpreting variations in individual mortalities.

Next, let us assume that all factors in the complex are density dependent so that, when we change one mortality, the absolute mortalities (d_x) caused by the other factors remain constant rather than their apparent mortalities ($100q_x$). If egg mortality decreases from 15% to 5% this mortality cannot be replaced by factors that follow, so generation survival is increased from 2 moths to 20 moths and $I=1,000$. If larval mortality decreases from 90% to 80%, generation survival becomes 3.4 and $I=170$. This difference in I caused by equal variations of 10% in apparent mortality, however, depends solely upon the sequence in which the factors operate. Let us say, for illustration, that egg mortality is normally 90% while larval mortality is 15%. A decrease of 10% in egg mortality still gives $I=1,000$ and a decrease of 10% in larval mortality still gives $I=170$. In other words, neglecting sequence for the moment, variations in individual mortalities have an equal effect on population trend regardless of the level of mortality at which they occur. This is quite a different conclusion from the one reached under the first assumption.

It is obvious, of course, that neither of these two assumptions is likely to be valid for a natural population. The mortality complex for most species includes both types of factors, which may operate contemporaneously or in sequence. Further, density relationships are unlikely to be simple, straight-line regressions and, as has been mentioned, they may operate only between certain limits of host density. The degree of parasitism caused by specific parasites in one generation, for example, depends not only upon the population of adult parasites that emerged from the preceding generation, but upon the relation between host density and parasite density. Thus the assumption that d_x will have a constant value regardless of preceding mortality in the same generation is not realistic. It is apparent, therefore, that *a priori* assumptions may give rise to erroneous interpretation and that proper interpretation must be based on a knowledge of the insect and its mortality complex, especially the density relationships, as obtained from a series of life tables. At the same time, it seems probable that the majority of factors affecting insect defoliators are of the density-independent type. If this were not so we would experience much more violent fluctuations from generation to generation than we do. This is obvious from

the examples presented in the last paragraph, where a decrease of only 10% in egg mortality resulted in a 10-fold increase in population ($I=1,000$). In the case of the spruce budworm we have so far detected a distinct density relationship only for larval parasites, at least up to the point where overpopulation phenomena begin to appear. In interpreting a given situation, therefore, it is necessary to recognize the *potential* hyperbolic influence of small variations in mortality when they apply to factors that normally give a high level of mortality. More specific conclusions can be reached only for individual cases, and no amount of arithmetic or algebraic manipulation with a 'mean' life table can provide real answers to biological or ecological questions.

The conclusions reached in this section are in agreement with those of Thompson in that a proper interpretation of mortality can be made only by recognizing the contrasting action of density-dependent and density-independent factors. It is pointed out here, however, in agreement with Bess, that the interpretation should be based on the relative changes in population trend rather than on generation mortality alone. The viewpoint expressed here is in disagreement with the general use of mortality/survival ratios for expressing the importance of individual mortality factors. The basic assumption that all factors are density independent is invalid for the spruce budworm, and probably for most insects. It is recognized, however, that the *majority* of factors are likely to be density independent in their action and that the potential effect of the M/S hyperbola should be kept in mind during interpretation and accepted where the basic assumption is satisfied. According to the conclusions of this section the viewpoint expressed by Bodenheimer (above) is untenable, for the importance of mortality is not in direct proportion to its magnitude.

The Order of Mortality

With regard to the order of occurrence, mortalities are sequential if they follow one another or contemporaneous if they occur together. It is apparent from the review of ideas in an earlier section that the effects of mortality factors acting in sequence have been treated in some detail by different authors, while the effects of contemporaneous mortalities have received little attention.

The question of sequence has already been touched upon in the preceding section. As in the case of the level of mortality, the importance of sequence depends entirely upon whether we are dealing with factors that are density independent or density related. If we assume density independence, it is clear that sequence has no importance. The mortalities in Table I may be re-arranged in any conceivable order without affecting generation mortality or population trend. Also, after re-arrangement, a variation in any mortality still has the same effect on generation mortality that it had before. Sequence, therefore, has no intrinsic effect and a given mortality or mortality variation is equally important in population dynamics whether it affects the initial egg stage or the final adult stage. Of course, sequence may be important from other points of view. The larval stage is generally the destructive stage so in an economic sense a high mortality operating before this stage is more important than one that comes after it. Also, a parasite that affects the egg or early larval stage must be able to reach a much higher absolute population than one that affects the pupal stage in order to give the same percentage mortality, and if alternate hosts are involved this may be of some importance. These are special problems, however, and do not affect the general conclusion.

If, on the other hand, we assume that the factors are density related, sequence becomes all-important. As illustrated in the last section, a variation in the

mortality affecting an early stage, such as the egg stage, has a vastly greater effect on generation mortality and population trend than an equal variation affecting a later stage.

This is another case, therefore, where proper interpretation can be made only for particular circumstances where the density relationships are fully understood. It is particularly important to recognize the fact that the apparent mortality caused by a density-dependent factor is related to the degree of mortality caused by other factors operating earlier in the sequence. Also, the degree of mortality that a given factor must cause in order to maintain a constant population level depends upon the magnitude and variation of other factors in the sequence. If M_1 and M_2 are two sequential mortalities, for example, we may be interested in knowing how much M_2 must vary in order to compensate for changes in M_1 and keep the population trend from changing. When the spruce budworm does not suffer from overpopulation, the factors operating before and after larval parasites appear to be largely independent of density. Therefore, if egg mortality increases from 15% to 50%, it may be calculated that a larval parasitism of 32% (in place of 40%) would maintain generation mortality at 99%. Similarly, in stands where dispersal loss is at its minimum of 60% a larval parasitism of 45% is required, but where dispersal loss is at its maximum of 95% only 10% larval parasitism is required. In the case of the normally low egg mortality, a variation of 35% has reduced the required larval parasitism only $40\% - 32\% = 8\%$ but an equal variation in the high dispersal mortality has reduced it $45\% - 10\% = 35\%$. As pointed out earlier, calculations of this type are mainly useful in suggesting lines of investigation and the results cannot be accepted as ecological facts. However, they demonstrate the principle illustrated in the last section and show that, when density-independent factors intervene, small changes in a high mortality have a disproportionately great effect on the changes that must occur in other mortalities if population increase is to be prevented. A general case can be plotted by using the first two terms of Thompson's basic formula for sequential mortality (quoted above), assuming a constant generation mortality of 99%, and solving for the second mortality in terms of the first. The resulting equation, $M_2 = 100[(99 - M_1)/(100 - M_1)]$ represents the same hyperbola that is already plotted in the upper part of Figure 1.

Contemporaneous mortality has implications that are even more important in population dynamics, as may be shown by considering a few examples from Table I. The apparent mortality in L_{3-6} averages 90%, which is made up of three mortalities that act contemporaneously—parasites 40%, disease 20%, and other factors 30%. According to the conclusions reached in the preceding section we should say that parasites are not likely to exert much influence on population trend because variations around a mortality level of 40% are relatively unimportant (cf. Fig. 1). However, if the other contemporaneous factors remain constant, variations in parasitism have the same influence on population trend as though they were taking place at a level of 90%. That is, if percentage parasitism increases from 40% to 45%, the effect on population trend is very great because the mortality affecting L_{3-6} increases from 90% to 95%. Therefore, in order to interpret the possible effects of the variations in mortality resulting from an individual factor, we need to know the level of mortality caused by the other factors that operate contemporaneously with it. This is a very important point that has not been adequately appreciated in the papers reviewed. If we compare the egg, larval, and pupal parasites of the spruce budworm, it is clear that egg or pupal parasitism would have to fluctuate widely in order to account for dynamic changes in population, because contemporaneous mortality is small.

On the other hand, comparatively small variations in larval parasitism could have a very drastic influence on population trend.

Recognition of the importance of contemporaneous mortality is important in the interpretation of mortality data for it suggests critical points in the life cycle and explains why variations in some seemingly unimportant mortality can determine population trend. In the actual interpretation of mortality data, it is desirable to have much shorter age intervals than those shown in Table I. The period L_{3-6} is a rather long and eventful one and encompasses a variety of both sequential and contemporaneous factors. When it is divided into four or more periods (Morris and Miller, 1954), it is seen that the individual periods may differ widely according to the level of contemporaneous mortality.

Mutual 'interference' among contemporaneous factors always adds difficulties to interpretation. In general, it will tend to reduce the important effects of contemporaneous mortality that have just been outlined. An increase in the degree of parasitism during L_{3-6} may be partially cancelled by the fact that some of the parasitized larvae would have died, in any case, from disease or other factors. Different *a priori* assumptions have sometimes been made concerning the degree of interference but it would seem safer to assess each situation individually on the basis of actual field data. Hardy (1939) presented a method for calculating the interference among the various factors affecting sawfly cocoons but his main assumption, which concerned the discriminatory abilities of small mammals, was later shown to be invalid (Morris, 1949; Holling, 1955). In order to combine mortality/survival ratios for contemporaneous factors, Bess had to make certain assumptions concerning interference. One of his main premises, that parasites cannot recognize larvae that are already parasitized, is quite invalid for the principal parasites attacking the spruce budworm.

The Expression of Mortality

Varley's example of the interpretation of mortality data was based on life tables for *Urophora jaceana*, and Morris and Miller suggested that the conventional life table columns would also be adequate for the spruce budworm. It is now proposed to consider the question as to whether interpretation can be aided by the use of additional columns for other methods of expression. The two possibilities that have been reviewed above are "real mortality" and "mortality/survival ratios".

The tabulation of real mortality in per cent would contribute little to the interpretation of the data in Table I. The figures would simply be the d_x figures multiplied by a constant, which, in the present case, would be 100/200 or 1/2. Any purpose that would be served by the percentage of real mortality would be served better by d_x because d_x represents actual numbers. It is true that summation in the real mortality column gives total generation mortality, but there are faster ways to calculate generation mortality using the l_x or the d_x columns.

A column for a fictitious real mortality is even less desirable. In this regard, Thompson's basic formula for real mortality (above) is sometimes used in a way that was probably never intended in order to calculate an "aggregate percentage mortality". Parasitism, for example, may be determined throughout the life cycle of an insect by dissections or rearings, and the data then inserted in the formula in order to calculate one "aggregate" percentage for the whole generation. With the egg, larval, and pupal parasites of Table I, this would be:

$$\text{Aggregate mortality} = a + (1-a)b + (1-a)(1-b)c \\ = .05 + (1-0.05)0.4 + (1-0.05)(1-0.4)0.1 = .487 \text{ or } 48.7\%$$

The real mortality actually contributed by parasites is, of course, $10/2 + 13.6/2 +$

$0.3/2=12.0\%$, or about one-quarter of that indicated by the aggregate percentage. The use of the formula in this way for any one factor ignores the fact that other factors are also operating and that the effect of the other factors may vary widely from generation to generation. Aggregate percentages are therefore of questionable value. They do not tell us whether the factor in question is increasing or decreasing in effectiveness from year to year, for they can be widely influenced by variations in other mortalities.

The tabulation of mortality/survival ratios is also of questionable value except, perhaps, for special purposes. It has been shown in earlier sections that the ratios themselves only suggest the potentialities of a given factor to influence population trend. If the apparent mortality caused by the factor is high but relatively constant, the high M/S ratio gives a misleading impression of its importance. It has also been shown that the ratios are not proportional to changes in survival population when density-related factors are involved. Again, the ratios for individual factors may be misleading because they ignore the important influence of contemporaneous mortality. Despite these weaknesses the ratios are of value in indicating potentiality and demonstrating the hyperbolic influence of high levels of mortality on population dynamics. As long as this relationship (Fig. 1) is kept in mind, however, tabulation of the ratios themselves may hardly be worth while.

As in the case of aggregate mortality, some workers who have used mortality/survival ratios seem to have the impression that they are magical transformations whose use, in some way, obviates the necessity of frequent population measurement and of attention to all mortalities. Bess, although admitting that population should be determined as frequently as practicable, encourages this viewpoint by stating, "However, estimates of the proportion of the population killed or affected by a particular factor are often obtained without procuring an estimate of the population density. Mortality/survival ratios derived from estimates of the proportion of the population killed may indicate the relative effects of different factors in the reduction of the abundance of an insect in a single generation, even though no estimates are obtained of the population of the insect when the factor or factors operated". This statement may be true but the key phrase "*in a single generation*" should not be overlooked. A combined mortality/survival ratio for one factor, such as parasites, cannot be used to show the relative effectiveness of the factor from generation to generation. It is subject to the same objections as aggregate percentage mortality and, because of variations in other mortalities, may provide very misleading conclusions as to the changes in parasite populations or effectiveness from year to year.

If we wish to understand population dynamics and to test the major theories on natural control, it seems that we cannot avoid the tedious necessity of frequent population sampling and life table development. Life tables, however, do not need to be developed indefinitely for one species. After a series has been obtained covering a wide range of conditions, it is quite possible that adequate interpretation may reveal one or two key factors that are mainly responsible for population changes. Concentration on these factors and disregard of relatively constant sources of mortality may lead to greatly simplified population work, supported as required by direct experimentation, behaviour studies, or other methods of approach.

Summary

Mortality data for natural populations are too often presented without adequate interpretation. One reason may be that the published ideas on the

interpretation of mortality are inadequate for the purposes of studies on population dynamics. Some of them are too much concerned with the progress of events within a single generation, and others with the relation of mortality to a single factor. In the present paper these earlier ideas are reviewed and an attempt is made to reach some conclusions affecting the interpretation of mortality in natural populations. It is concluded that variation is the important attribute of mortality and that low but variable mortalities may therefore have more influence on population trend than high but relatively constant mortalities. Although density relationships are important, it is necessary to study the relation of mortality variations to other extrinsic and intrinsic factors in order to understand population dynamics. The concept of "indispensable" mortality has only a limited application; natural factors may cause a relatively constant mortality or a mortality that varies within certain limits but seldom do they disappear from the complex, or new factors appear, except through man's intervention. Variations in individual mortalities should be interpreted according to their effects on population trend rather than on generation mortality alone, the relationship between population trend and generation mortality being hyperbolic rather than directly proportionate (Fig. 1). Variations that occur at high levels of mortality may have an effect on population trend that is greater than or equal to the effect of similar variations at low levels of mortality, depending upon density relationships. Since most mortality factors appear to be density independent, however, it is essential in interpretation to keep in mind that variations at high levels are potentially more important, the relative influence being represented by a hyperbolic function. The importance of the sequence in which different mortalities occur is also dependent upon density relationships and more specific conclusions can be reached only for individual situations where these relationships are understood. The magnitude of mortality contributed by contemporaneous factors is extremely important and serves to explain why it is possible for a low but variable mortality to act as the primary determiner of population trend. It is also concluded that the columns of the conventional life table will generally provide an adequate means of expression to serve as the basis for mortality interpretation.

Acknowledgments

For the critical examination of the ideas expressed in this paper I am indebted to many associates in the Forest Biology Division. In particular I wish to thank Mr. C. A. Miller, my colleague on the Green River Project; Dr. R. E. Balch, Officer-in-Charge of the Fredericton Forest Biology Laboratory; Dr. M. L. Prebble, Chief, Forest Biology Division; and Dr. W. G. Wellington, Head, Bioclimatology Section.

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Insects Affecting Seed Production in Red Pine
II. *Dioryctria disclusa* Heinrich, *D. abietella* (D. and S.), and
***D. cambiicola* (Dyar) (Lepidoptera: Phycitidae)¹**

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Introduction

This paper describes the seasonal history and habits of three borers of the genus *Dioryctria* that destroy red pine cones in Ontario. These insects, as a group, generally rank second in importance as cone destroyers to the cone beetle, *Conophthorus resinosae* Hopk., which was the subject of the first paper in this series (11), and are presented together because of their family relationship and the similarity of their habits.

Representatives of the genus *Dioryctria* feed on conifers in the northern hemisphere. Most species are restricted geographically and in number of hosts, and to one or two parts of the host tree (cones, shoots, etc.), although *D. abietella* (D. and S.) is holarctic in distribution and indiscriminate in feeding habits. A few species reach economic importance by damaging valuable trees, e.g. *D. zimmermani* (Grt.) in the United States (3) and *D. splendidella* H.S. in Europe (5). *D. reniculella* (Grt.) as well as feeding on the foliage of spruce (2), is a predator of the spruce budworm, *Choristoneura fumiferana* (Clem.) (17). Many *Dioryctria* species attack the cones of pines and other conifers, and sometimes cause heavy damage, e.g. *D. auranticella* Grt. in western North America (6), *D. amatella* Hlst. in the southern United States (16), and the species discussed in this paper.

D. disclusa, *D. abietella*, and *D. cambiicola* were all more common in southern Ontario than elsewhere in the Province during the period of this study (1950 to 1954). *D. disclusa* and *D. cambiicola* damage cones primarily during June and July, but *D. abietella* is active throughout the growing season, and cones may be damaged by it throughout an extended period. All species tunnel into cones, but there are differences in the mode of cone damage that usually enable them to be recognized. They are also distinguishable by their physical appearance. The scarcity of these insects has made them rather difficult to study adequately, but during the summer of 1953 about 50 adults of *D. disclusa* were obtained through rearing, and this made possible the observation of adult activity, oviposition, and the behaviour of young larvae. Only a few adults of *D. abietella* and *D. cambiicola* were ever available at one time, so these species could not be intensively studied. The descriptions of larvae of *D. disclusa* and *D. abietella* are based on good series of preserved larvae, but that of *D. cambiicola* is based on only a few specimens and is consequently incomplete. Fracker's (9) system of setal nomenclature is used throughout.

***Dioryctria disclusa* Heinrich**

D. disclusa infests second-year red pine and jack pine cones in many parts of Ontario, but is seldom as destructive as the cone beetle, *Conophthorus resinosae*. Until recently it was referred to as *D. auranticella* Grote. However, according to Heinrich (in 7), *D. auranticella* is a western species and synonymous with *D. xanthobenobares* Dyar, whereas *D. disclusa* is confined to eastern North America, where it is found west to Iowa and south to North Carolina. There is only one generation per year, cone damage occurring during May and June

¹Contribution No. 283, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

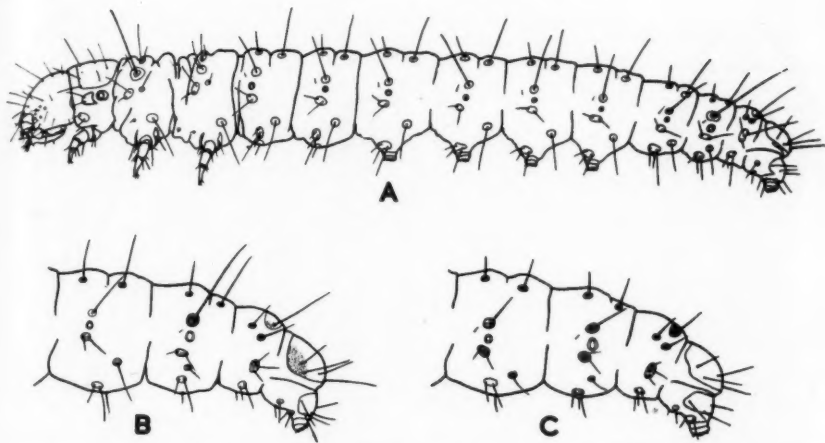


Fig. 1. Larvae of *Dioryctria* spp. from red pine cones. A. *D. disclusa* Heinrich; B. *D. abietella* (D. and S.); C. *D. canbucola* (Dyar).

in Iowa (7), and during June and July in Ontario. Farrier and Tauber (7) have discussed the activity of *D. disclusa* in cones of Scots pine in Iowa, but their description of the larvae and some details of the life history differ from those of the insect in Ontario. These differences are pointed out in the following description.

Description of Developmental Stages

Egg

The egg of *D. disclusa* in Iowa, as described by Farrier and Tauber (7), is white, elliptical, 1.0×0.75 mm. in size, and without sculpturing on the surface. This is considerably larger than the eggs found during the present investigation, which were about 0.45×0.37 mm. in size, with the surface finely roughened. The larva is clearly visible before hatching, and imparts a reddish colour to the egg. The empty chorion is colourless and transparent.

Larva

The mature larva of *D. disclusa* (Fig. 1A) is a slender, olive-green to buff caterpillar, 14 to 18 mm. long, with lighter patches dorsally and laterally on each segment. There are five instars, the mean head widths of which are: instar I, 0.26 mm.; instar II, 0.40 mm.; instar III, 0.57 mm.; instar IV, 0.92 mm.; and instar V, 1.44 mm. The approximate length of preserved larvae is: instar I, 2-3 mm.; instar II, 3.5-4.5 mm.; instar III, 4-7 mm.; instar IV, 8-12 mm.; and instar V, 13-18 mm. Larvae in Iowa differ from those encountered during this investigation in being considerably larger (mature larva: head width about 4.5 mm.; body length, 17-27 mm.), and in lacking colour pattern on the body (7).

Head: varying from pale yellow-brown to dark orange- or chestnut-brown; genal markings varying from pale indistinct to dark brown distinct; mandibles reddish in newly eclosed larvae, later blending in colour with rest of head.

Thorax: pronotum grey-brown to orange-brown, mottled with black in mature larvae; legs pale in young larvae, later darkening; seta rho of mesothorax conspicuously longer than others, inserted in a ringed sclerite rather than a solid one; Kappa setal group of prothorax occasionally trisetose rather than bisetose.

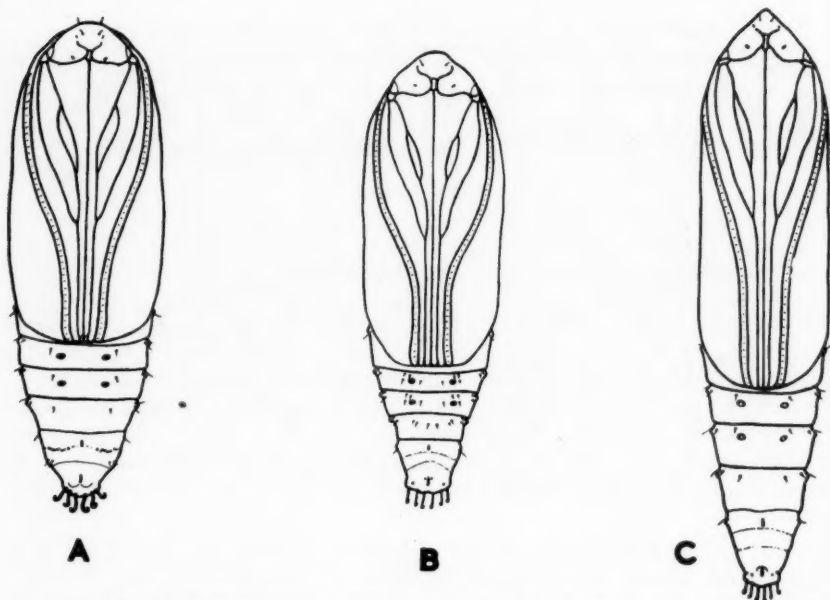


Fig. 2. Pupae of *Dioryctria* spp. from red pine cones. A. *D. disclusa* Heinrich; B. *D. abietella* (D. and S.); C. *D. cambicola* (Dyar).

Abdomen: segmentation distinct; setal sclerites in instars I to IV usually concolorous with rest of body surface, those of instar V dirty white to brilliant white; seta rho of eighth segment conspicuously longer than others, inserted in a ringed sclerite; proleg crotchets of instars I and II uniserial and uniordinal, those of instars III to V uniserial and biordinal; epiproct light brown.

Abdominal coloration: Instar I, 11 broken longitudinal stripes on each abdominal segment, purplish-brown on pale brown background; instar II, stripes not so broken but less distinct, faint purple on pale brown or white background; instar III, an irregular longitudinal line through bases of setae alpha and beta, another but less distinct line through space between spiracle and seta rho (above spiracle), white on pale brown background; instar IV, dorsal and subdorsal stripes varying from distinct to faint, or almost absent; background dark green in young larvae, becoming buff in old ones, some larvae tinged with red on thorax and abdomen; instar V (Fig. 1A): background light olive-green to dark purple-brown; longitudinal stripes faint and grey, often almost lacking, most distinct on palest larvae; each segment marked with a pale surrounding and connecting setae alpha and beta, another pale patch surrounding spiracle and seta rho, sometimes tinged with red, especially on darker larvae, and a third pale patch surrounding Kappa group of setae (below spiracle); ventral surface paler than dorsal.

Pupa

The pupa (Fig. 2A) is 9-14 mm. long, robust, heavily sclerotized, mahogany brown, bluntly rounded anteriorly, with thick, lyre-shaped caudal hooks.

Adult

The adult of *D. disclusa* is a bright white, orange, and red moth with a wing expanse of 21-27 mm. The specimens described by Heinrich (in 7) had a wing



Fig. 3. Successive stages in red pine cone damage by *Dioryctria disclusa* Heinrich.

expanse of 24-29 mm., but were from localities south of Ontario. The forewing markings are variable, but usually the basal quarter to third is orange, separated by a broken transverse white line from the reddish-brown remainder of the wing. The longitudinal streak between the second and third white transverse lines varies from white to reddish-orange. The reniform spot is usually inconspicuous and is almost absent in the darkest individuals. The hind wings are brownish-grey.

Seasonal History

D. disclusa spends the winter as a first-instar larva in a thin, flat hibernaculum beneath the bark scales of red pine branches. The exact time of emergence from hibernation is not known, but first-instar larvae were found boring in immature red pine staminate flowers in late May. The larvae remain in staminate flowers until about the time of pollen shedding, when the third- and fourth-instar larvae migrate to, and attack, second-year cones (early June to mid-June, when the cones have attained about half their final length). Farrier and Tauber (7) found what was believed to be a second-instar larva tunnelling in pine cones in Iowa in late May.

On attacking the cone, the larva almost invariably bores a conspicuous hole in the underside near the petiole, but does not seem to ingest the cone cuticle, which remains as a small ridge surrounding the entrance hole. As the larva tunnels into the cone, ejected frass pellets are trapped by a silk net spun between the cone and nearby needles and eventually accumulate into a conspicuous reddish-brown mass. The larva gradually excavates the seed-bearing region of the cone (Fig. 3), and the resulting cavity may become partially filled with resin, particularly in large cones. If the cone axis becomes severed, as is usually the case, the cone soon withers and eventually becomes hard and brown. Cones that are unsuccessfully attacked may survive and produce seeds, but most cone attack

is fatal. Each larva probably attacks two cones, moulting to the fourth instar in the first, and completing development in the second.

The mature larva ceases feeding in July and, before pupating, spins a circle of silk across and slightly inside the entrance tunnel, and a thin silk cocoon about itself. It then becomes shorter and thicker, often taking on a distinct greenish hue, especially about the thorax, and pupates facing the tunnel exit. The pupa is at first yellowish-white, but soon darkens. Under natural conditions, pupae were found only in damaged cones, but this may not necessarily be the only site of pupation. In rearing, many larvae left the cones before pupating, and they may, presumably, do so in the field also.

According to rearing records, the duration of the pupal stage at Angus, Ontario, in 1953 was 15 to 21 days. Adult emergence began about mid-July and was virtually complete by August 1. The peak emergence period of males was July 16-18, about five days earlier than that of females. The empty pupal case is firmly retained inside the cone, and is seldom seen unless the cone is cut open.

To study the habits of adults and to determine where eggs were deposited, pupae were placed in wire screen cages (about 2.0' x 1.5' x 1.5' with a removable top) in which were suspended red pine branches connected by a rubber hose to a supply of sugar and water. The activity of the two dozen adults that subsequently emerged was noted at intervals. To supplement those observations, adults from reared pupae were separated into pairs (a male and a female), and placed in cloth-topped pint sealers containing a pleated piece of moistened paper towelling. The number and condition of adults, eggs, and larvae were recorded each day.

The only two matings that were observed began about 11.00 p.m. EST, and continued until after 12.30 a.m., but some females assumed a pre-mating posture, i.e. extending and elevating the abdomen, as early as 10.00 p.m. Adults of both sexes remained inactive during daylight. Caged adults were kept under observation until about 1.00 a.m. on several nights, but no female was seen ovipositing. Male adults lived about 9 days, and females about 12. Most females laid between 10 and 55 eggs, but a few laid well over 100. The caged foliage was removed when the adults had died. A careful search revealed that almost all eggs and hibernating larvae were located beneath bark scales on needle-less parts of the branch that were six to nine years old. The larvae had apparently not wandered far after eclosion, and had probably spun their thin, flat, white, hibernacula at the first opportunity. There was no evidence that they had fed. In the rearing jars most eggs were situated in crevices of the pleated paper towelling, and the larvae shortly after eclosion spun hibernacula in enclosed places, e.g. where the paper touched glass. In August, 1953, at Angus, several branches from a tree, whose cones had been attacked by *D. disclusa*, were thoroughly searched for hibernating larvae. The few larvae found were all beneath bark scales on needle-less parts of the branches.

Natural Control

Owing to the relative scarcity of *D. disclusa* in many localities during most of this investigation, it was not possible to gather extensive information on the natural control of this important cone insect. Most of the mortality observed was due to parasitism.

Mortality from parasitism was heaviest during the pupal stage. Of 66 pupae collected at Angus in 1953, 32 were parasitized and eight contained dead *D. disclusa* adults, with about 85% of the parasitism being caused by *Coelichneumon*

sp. (Ichneumonidae), and the remainder by *Dibrachys cavus* (Wlkr.) (Pteromalidae). *Coelichneumon* sp. overwintered as a larva in the host pupal case and emerged as an adult in late spring. It, in turn, was parasitized by *Amblymerus verditer* (Nort.) (Pteromalidae), adults of which also emerged in late spring. Adults of *D. cavus* emerged from *D. disclusa* pupae in late summer. There may be as many as two dozen parasites of this species per host, but seldom more than two or three emergence holes. Females of *D. cavus* are entirely black and about 3 mm. long, and are larger and more numerous than males, which have a greenish frons and brownish antennae.

Four parasitic species were reared from *D. disclusa* larvae at Angus in 1953. *Microtypus* sp. and *Calliephialtes comstockii* (Cress.) (Hymenoptera: Ichneumonidae) emerged from third- and fourth-instar larvae of *D. disclusa*; adults of the former appeared in early July, and those of the latter in late July. Larvae of *Bracon rhyacioniae* Mues. (Hymenoptera: Braconidae) emerged from mature larvae of *D. disclusa* during late July and pupated nearby in white cocoons. An undescribed tachinid parasite was reared from maggots that emerged from mature *D. disclusa* larvae in early July; adults appeared about two weeks after pupation. According to G. E. Shewell, Insect Systematics and Biological Control Unit, Entomology Division, Ottawa, this parasite, previously identified as a "new genus near *Oxynops*", has been consistently reared by the Forest Insect Survey from *Petrova albicapitana* Busck.

Raizenne (14) reared *Meteorus indagator* (Riley) (Braconidae) and *Horogenes* sp. (Ichneumonidae) in 1946 and 1948, respectively, from *D. disclusa* in Simcoe County, Ontario, but neither species was recovered during the present investigation. Six ichneumonid and four braconid parasites have been reported from *D. disclusa* in Iowa (7), but only one of these, *Calliephialtes comstockii* (Cress.), was recovered from *D. disclusa* in Ontario. Apart from the mention by Farrier and Tauber (7) of a few non-parasitized pupae failing to produce adults, there seems to have been nothing published on mortality by other factors.

Dioryctria abietella (D. and S.)

D. abietella infests the cones, shoots, and bark of many different conifers, and is apparently holarctic in distribution (12). Specimens in the United States National Museum, according to J. F. Gates Clark, Curator, Division of Insects, are from *Abies* spp., *Pseudotsuga menziesii* (Mirb.) Franco, and all *Pinus* spp. in North and Central America, British Columbia, and Labrador south to Guatemala. According to de Sandt (5), the damage by this species in France was long confused with that by *D. splendidella* (H.-S.) and *D. mutata* (Fuchs), a pitch borer and a cone borer, respectively. A similar confusion has existed in North America between *D. abietella* and *D. reniculella* (Grt.) (12), although larvae of the two species are easily distinguishable. Some of the habits of *D. abietella* have been described by Craighead (4), Packard (13), Keen (10), and Doane et al. (6).

D. abietella played only a small part in red pine seed loss in Ontario from 1950 to 1953, but caused considerable damage during 1954. There is apparently only one generation per year in Ontario, but larvae are active throughout the summer, although Keen (10) suggests the possibility of two generations per year in the western United States.

Description of Developmental Stages

Egg

Only a few unfertilized eggs were observed. These were white, oval in outline, flattened, about 1 mm. long, with the surface finely roughened.

Larva

The typical mature larva of *D. abietella* is longer (15-25 mm.) and less robust than that of *D. disclusa*, and is reddish-purple with paler dorsal and longitudinal lines. There are five instars, the approximate head widths of which are: instar I, 0.45 mm.; instar II, 0.71 mm.; instar III, 1.10 mm.; instar IV, 1.35 mm.; and instar V, 1.70 mm.

Head: grey-brown in young larvae but later varying from pale brown to dark brown, marked genally, and smooth.

Thorax: pronotum grey-brown in young larvae but darker than head, in older larvae light brown medially, darkening laterally and anteriorly; seta rho of mesothorax conspicuously longer than others, inserted in a ringed sclerite; legs pale.

Abdomen: setal sclerites grey-brown, conspicuous in young larvae but less so in older ones; seta rho of eighth segment longer than others, inserted in a ringed sclerite; proleg crotchets of instar I uniserial and uniordinal, those of instars II to V uniserial and biordinal; epiproct pale brown in young larvae, later becoming yellowish-brown medially with darker areas laterally and anteriorly (Fig. 1B).

Abdominal Coloration: instars I and II white to grey, without stripes or markings; instars III and IV pale red to dark purple, sometimes faintly lined dorsally and subdorsally, instar V pale red to dark purple brown, sometimes with bright red in spiracular region; young larvae more distinctly striped than others, with a narrow mid-dorsal stripe and a wider sub-dorsal stripe; prepupae often tinged with green, especially on thorax.

Pupa

The pupa (Fig. 2B) is 10-12 mm. long, more slender and delicate than that of *D. disclusa*, pale brown, rounded anteriorly, with straight, slender caudal hooks.

Adult

Adult *D. abietella* from red pine cones are as described by Ratzeburg (15), Packard (13) (under the name *D. reniculella*), and MacKay (12). The forewing is predominantly grey, with transverse, white, zigzagged lines bordered by black. Some specimens have a few reddish scales on the wings and shoulders. Wingspread of adults from red pine cones varied from about 23 mm. to about 28 mm., agreeing substantially with specimens described by Forbes (8), but being smaller than those described by de Sandt (5) in France (28-32 mm.), and somewhat larger than the one male (22 mm.) described by Packard (13).

Seasonal History

D. abietella has been reported as overwintering in several different stages; partly grown larvae (4), prepupae (12), and pupae (2). Specimens from white spruce in Canada have an early and a late flight period (2). Raizenne (14) reports that *D. abietella* from spruce and pine cones in southern Ontario are most common as adults in August and October, and as larvae in June and September, but that both stages are present during the intervening months.

This overlap in generations was also detectable in *D. abietella* in red pine cones. All five larval stages were represented in some samples in July. Larvae maturing in July and August transformed to adults in late summer, and their progeny probably overwintered as young larvae. Some larvae that matured in September became adults several weeks later, while others spent the winter as pupae or prepupae in thin, debris-coated cocoons, emerging as adults the following spring.

Damage to red pine cones usually begins early in July, and continues until late August or early September. Young larvae feed primarily between the deteriorating scales of second-year cones previously damaged by other insects, but older ones are capable of attacking fresh cones. Third- and fourth-instar larvae tend to enter at the extreme base of the cone, close to the petiole, and tunnel through young seeds close to the cone axis. Fifth-instar larvae do not penetrate the cone so deeply, but remain close to the surface and feed on the spongy tissue of the scale tips. There are sometimes as many as 10 *D. abietella* larvae per cone, but some of these are usually young ones feeding secondarily. Mature larvae migrate readily from one cone to another, spinning silk between a nearby surface and the new cone before entering. The mature feeding larva keeps its tunnel clear of frass and debris, and can move about freely within the cone, or, if alarmed, withdraw rapidly. Larvae in rearing usually leave the cone to pupate.

No eggs were found in natural conditions, but a few females oviposited on second-year cones in glass jars. The eggs were invariably deposited singly in the shallow crevices between adjacent cone scales.

Natural Control

During 1954, the year that *D. abietella* was most abundant in red pine cones, the only mortality observed was due to parasitism. Adults of *Elachertus* sp. (near *proteoteratis* How.) (Hymenoptera: Eulophidae) were reared from seven pale blue-green larvae that emerged from one mature *D. abietella* larva collected at Thessalon, Ontario. The parasite larvae formed naked, black pupae about 1 mm. long near the dead host. Adults emerged in the laboratory after having been held several months in cold storage, and under natural conditions would probably have emerged the following spring or summer. One adult of the same undescribed tachinid ("new genus near *Oxynops*") that parasitizes *D. disclusa* was reared from a *D. abietella* larva at Midhurst.

Dioryctria cambiicola (Dyar)

During the investigation of red pine cone insects, *D. cambiicola* was found infesting red pine shoots as well as second-year cones in the Lake Simcoe region, but was rare compared to *D. disclusa* and *D. abietella*. According to Brunner (3), *D. cambiicola* in Montana and Idaho infests the cambium of the terminal branches of *Pinus ponderosa* Dougl., and, although the effect of infestation by *D. cambiicola* itself is slight, the damaged branches are subsequently reinfested by *Dioryctria zimmermani* (Grt.), which is capable of killing or severely stunting infested trees. Atwood (1) records that *D. cambiicola* in 1943 destroyed 25% to 35% of the buds and new shoots in a red pine plantation in Wellington County, Ontario. The United States National Museum records *D. cambiicola* from *Pinus ponderosa* and *P. coulteri* D. Don. in Montana, Colorado, New Mexico, Arizona, and California.

Description of Developmental Stages

Egg

No eggs were observed, and there seems to be no published description of them.

Larva

The mature larva is a sluggish, grey to green caterpillar about 15 mm. long, with prominent dark sclerites. The following description is based primarily on mature larvae.

Head: light brown in young larvae, but later darkening; width in mature larva about 1.7 mm.

Thorax: pronotum orange-brown to dark brown; seta rho of mesothorax about same length as others, inserted in a ringed sclerite; legs dark brown.

Abdomen: setal sclerites light brown in young larvae but later darkening, larger and more conspicuous than those of *D. abietella*; setae shorter and thicker than those of either *D. disclusa* or *D. abietella*; seta rho of eighth segment no longer than others, inserted in a solid sclerite rather than a ringed one (Fig. 1C); epiproct paler than setal sclerites, white in young larvae but later varying from grey to dark purple-brown or bright green.

Pupa

The pupa (Fig. 2C) is 12-15 mm. long, slender, pointed anteriorly, with straight, slender caudal hooks.

Adult

The wing expanse of *D. cambiicola* adults collected from red pine cones and shoots varies from 21 mm. to 30 mm. The forewing is dark purple-brown with several pale transverse lines, the inner two of which are bounded on the outside by a tufted row of black scales. The hind wing is smoky-brown.

Seasonal History

The seasonal history of *D. cambiicola* in red pine resembles that of *D. disclusa*, in that larvae and adults are active at about the same time. However, *D. cambiicola* larvae apparently feed primarily in the pith of large current-year's red pine shoots, and attack cones only when nearly mature. Cone damage in 1953 occurred in late July, and closely resembled that by *D. disclusa*, i.e. a large entrance hole in the side of the cone. The cavity inside the cone, however, was much smaller than that made by *D. disclusa*. Larvae feeding in shoots were usually difficult to find because, by the time the infested shoots became brown and conspicuous, i.e. in mid-summer when the needles were about half grown, the mines contained only empty pupal cases. Hence, to collect larvae it was necessary to search through large numbers of apparently undamaged shoots.

In rearing, mature larvae were much more sluggish than those of *D. disclusa* or *D. abietella*, and seemed to be less liable to leave the cone or shoot before pupation. In 1953, adults appeared in late July and early August, one to two weeks later than those of *D. disclusa*. No progeny of these adults were obtained, but according to Raizenne (14), *D. cambiicola* overwinters in the larval stage.

Natural Control

Two mature larvae of *D. cambiicola* in red pine shoots at Camp Borden were found to be parasitized, one by *Hyssopus rhyacioniae* Gahan (Hymenoptera: Eulophidae) and the other by the same tachinid ("new genus near *Oxynops*") that parasitizes *D. disclusa* and *D. abietella*. According to F. P. Keen, California Forest and Range Experiment Station, *D. cambiicola* in California is parasitized by *Campoplex conocola* (Roh.) (Hymenoptera: Ichneumonidae).

Acknowledgments

Sincere thanks are due the Insect Systematics and Biological Control Unit, Entomology Division, Ottawa, for identification of insects; R. W. Fassold for assistance during the field season of 1953; D. C. Anderson for the photographs; and the staff of the Forest Insect Laboratory for criticism of the manuscript.

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(Received June, 1956)

A Note on the Occurrence of *Sipha agropyrella* Hille Ris Lambers (Homoptera: Aphidae) in Manitoba

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On October 16, 1956, during a routine monthly check of the Nurses Residence, Selkirk Mental Hospital, Selkirk, Manitoba, a professional exterminator noticed "thousands" of very small insects in a basement office. A number were submitted to the writer for identification and found to be aphids, which were later very kindly identified by W. R. Richards, Insect Systematics and Biological Control Unit, Ottawa, as *Sipha agropyrella* (H.R.L.). Richards stated (in litt.): "This is the first record of this species west of Ontario." MacGillivray (1956) records the finding of this species in 1950 in New Brunswick as a new record for North America.

It was not possible to determine the host plant at this time. Aphids were crawling over papers, desks, furniture and walls in the basement office, and over the window sill. Outside they were even more numerous on the wall, and on blades of grass of the lawn. All the individuals collected were oviparae. It is unusual for aphids, particularly oviparae, to enter buildings.

This distribution record raises the question of whether this is an introduced species moving westward in Canada, or an indigenous species hitherto unrecorded.

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Studies on Nervous System Anatomy of the Douglas Fir Beetle, *Dendroctonus pseudotsugae* Hopk. (Scolytidae)¹

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This paper describes the main anatomical features of the adult nervous system of the Douglas fir beetle, *Dendroctonus pseudotsugae* Hopk. The study on which it is based was carried out to provide a background for further work on the nervous system and as part of a program of investigation of the physiology and behaviour of scolytid beetles.

Extensive comparative studies of coleopterous nervous system were made long ago by Blanchard (1846) and Brand (1879). Their descriptions of scolytid material are sketchy and brief, however, and because we can find no other treatment of the nervous system in the Scolytidae we are presenting this brief report on our work.

Our objective was to determine the pattern and relationships of the ganglia and nerve trunks. Accordingly, except in the case of the reproductive system, the branching and pathways of the nerves themselves received little attention and we did not attempt to make a detailed study, such as that of Holst (1910) on *Dytiscus*, for example. The insectan nervous system is treated quite extensively by Snodgrass (1935), whose terminology we use unless otherwise indicated, and also in a number of general entomological works (e.g., Schröder, 1928; Imms, 1951; Weber, 1954). For this reason we describe the general features of the Douglas fir beetle nervous system primarily by drawings, and comment or discussion is given only for features of particular interest or importance.

Freshly killed insects were used for most dissections and proved to be more suitable than preserved material in that the body organs could be separated more easily and the nerves were more flexible and could be handled more without breaking. Dissections were made under saline solution, using 27x and 54x magnifications for the most part. The difficulty of seeing the smaller nerves and branches against the white tissue and organs characteristic of fresh insect material was overcome by staining the nerves with Delafield's Haematoxylin. This was added with a fine-tipped pipette to areas under examination and then quickly rinsed off. It was noted that nerves of old beetles were more opaque than those of young adults and because there was also less interference from the fat body in the former they were more suitable for the purpose.

The relative position of ganglia and nerve trunks in this insect is shown in Fig. 1. Blanchard (1846) figured the nervous system in 41 beetles representing some 30 families, and studied many more. According to him the prothoracic ganglia are always separate from those of the meso- and metathorax in the Coleoptera. Brand (1879), however, examined the nervous system in 235 species of beetles and reported that in some lamellicorns only a single fused thoracic ganglion was present. With respect to abdominal ganglia, the scolytids are similar to curculionids and lamellicorns in having a single fused mass, closely joined with the meso- and metathoracic ganglia. Within the Coleoptera the number of separate pairs of abdominal ganglia varies from one to eight and most beetles have two or more. The consolidation of these ganglia in scolytid beetles indicates a high degree of specialization as it represents a considerable

¹Contribution No. 319, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

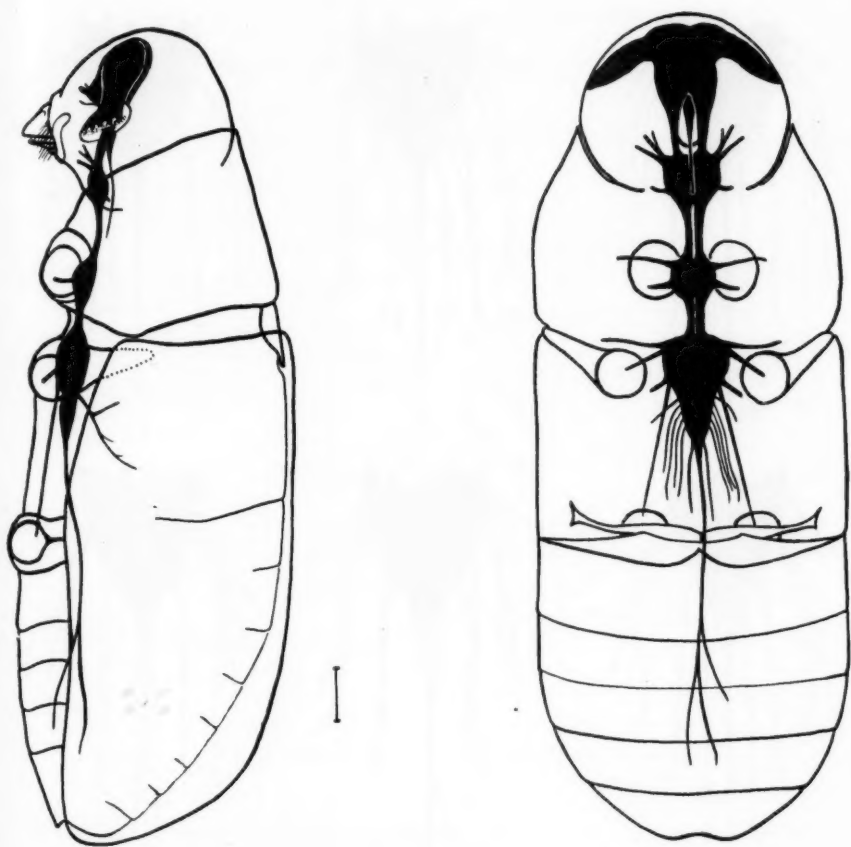


Fig. 1. Position of ganglia and nerve trunks in the body.

change from the primitive condition in which a pair of ganglia occurs in each abdominal segment (e.g., Beier, 1927).

An interesting degree of variability, possibly a consequence of the fusion of ganglia, was found in the way in which the abdominal nerve trunks originate and also in their branching. The former type of variability is illustrated in Fig. 2. It is best explainable, we believe, by assuming differences in the way the sheath material or enurilemma encloses the nerve fibres rather than in the ultimate course of the fibres. Thus two adjacent nerve trunks may leave the ganglionic mass separately, or together, in which case a later branching occurs. Or, apparently, a bundle of nerve fibres sometimes leaves the fused ganglia by one nerve trunk and later joins another. Variations in branching, explainable on the same basis were particularly frequent in nerves of the reproductive system. Blanchard mentioned some differences in nerve trunk branching and Hertweck (1931) described slight variations in *Drosophila* nervous systems. The extent

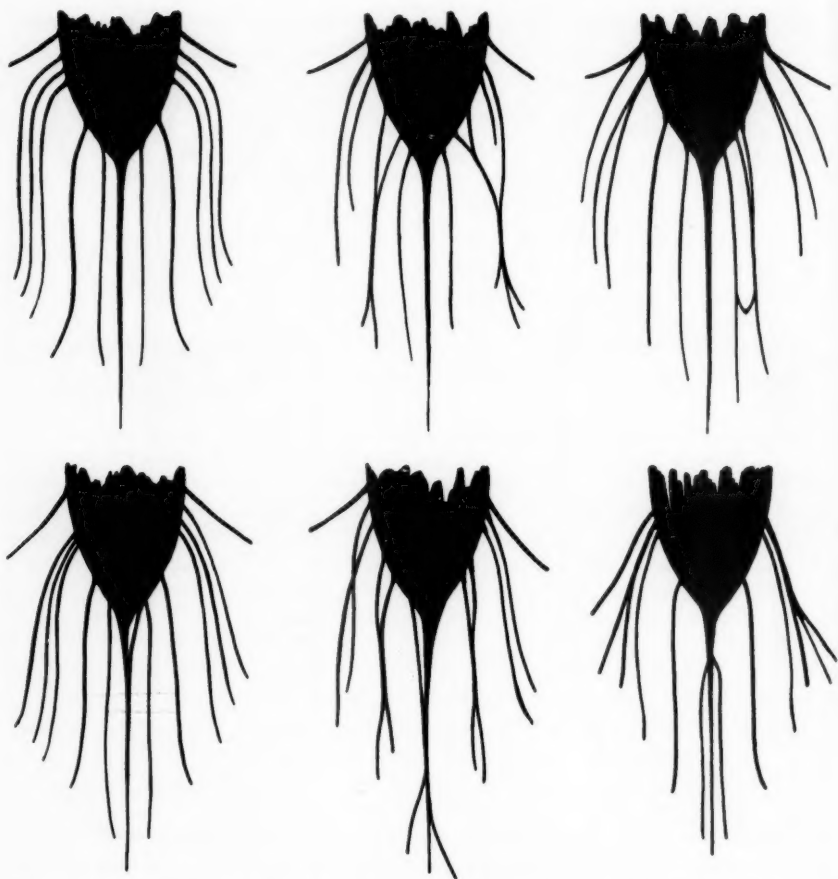


Fig. 2. Variability in origin and branching of abdominal nerve trunks illustrated by some of the arrangements encountered.

of differences between individual Douglas fir beetles with reference to features mentioned above, however, was relatively great and was sufficient to cause some confusion in the early stages of the work.

Fig. 3 presents a dorsal view of the nervous system and its major thoracic and abdominal branches and Fig. 4 shows further details of the head ganglia and nerves, including the main parts of the stomatogastric nervous system and the retrocerebral endocrine complex. A few comments are in order with respect to terms used in these figures. The suboesophageal or substomodaeal (tritocerebral) commissure is referred to as the post-oesophageal commissure by Imms (1951) and the stomodaeal commissure by Henry (1948). The procurrent nerve, running anteriorly from the frontal ganglion is so designated by Weber (1954). Nerves from the posterior lateral part of the suboesophageal ganglion are apparently not a constant feature of insect nervous systems for they are not usually

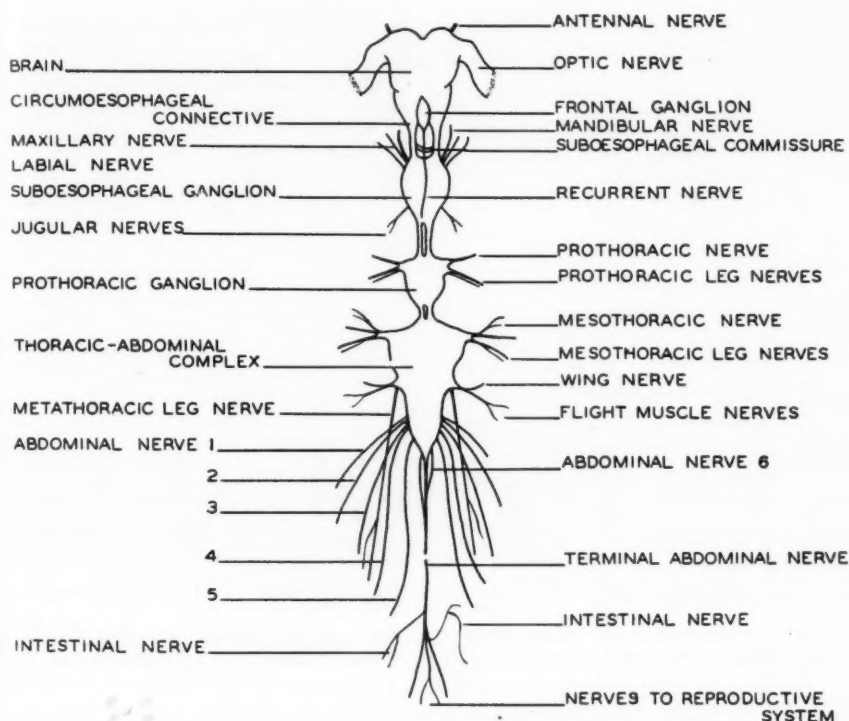


Fig. 3. Dorsal view of the central nervous system.

named or described. Although Snodgrass (1935) refers to a cervical nerve from this region we follow Holst (1910) who carefully described and figured the nervous system of a beetle, *Dytiscus*, and used the term jugular nerves for those in this region. Korschelt (1923) presented Holst's findings again.

The stomatogastric (stomodaeal; anterior sympathetic) nervous system comprises the frontal ganglion with its connectives, the procurrent and recurrent nerves, the hypocerebral ganglion when present, and the ventricular ganglion with its branches. The retrocerebral endocrine system includes the *Corpora cardiaca* (*C. paracardiaca* of Cazal, 1948) *Corpora allata* and their associated nerves. These two systems are closely related and have been investigated quite intensively in various insects within the past decade because of increasing interest in the source, function and control of hormones in insects. Because of this, we follow Weber (1954) rather than Snodgrass (1935) with respect to terminology in these systems.

The unusual position of the frontal ganglion in the Douglas fir beetle will be noted immediately by anyone familiar with the nervous system of insects. All descriptions or diagrams we have seen of this structure in beetles or other insects place it in a more anterior position, with considerably longer frontal connectives. Blanchard, speaking of coleopterous nervous systems, stated that it is always anterior to the brain. Neither his diagram nor descriptions of the scolytid

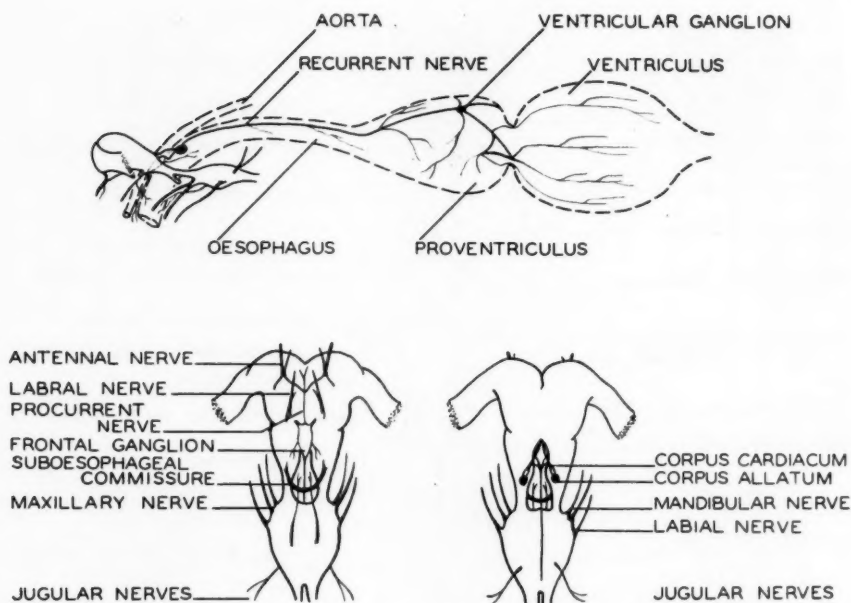


Fig. 4. Ganglia and nerve trunks of head region, and retrocerebral endocrine system. Lateral, ventral, and dorsal views (above, below left, and right, respectively).

system give details for the head region, however. Actually in the Douglas fir beetle the frontal ganglion is largely posterior to the brain and the frontal connectives are very short and are not as closely associated with the labral nerves in their origin as in most insects.

There are nerve connections between the frontal ganglion and the *Corpora cardiaca*, but we found nothing resembling a hypocerebral (median occipital) ganglion along the course of the recurrent nerve. Blanchard indicated that in beetles the recurrent nerve typically enlarges slightly, posterior to the brain, to form a small elongate ganglion (the hypocerebral ganglion) connected with the heart ganglia (*C. cardiaca*) by means of two fine strands. Brand did not mention such a ganglion in his brief description of the stomatogastric nervous system of beetles. Holst did not find any gangliar swelling along the recurrent nerve in *Dytiscus* but stated that branches of this nerve led to the heart ganglia (*C. cardiaca*) and apparently joined with them. Hanström (1928) stated that the existence of the hypocerebral ganglion is variable within the insects and mentioned that it is present in some beetles but absent in *Dytiscus*. Weber (1954) presents this ganglion as a typical feature of insect nervous systems. It appears that the hypocerebral ganglion, when it exists, is usually the site of connections between the *C. cardiaca* and the stomatogastric nervous system. Cazal (1948) included 11 beetles in his comprehensive study of the insect retrocerebral endocrine system but no curculionids or scolytids were represented. He did study *Melolontha*, a lamellicorn beetle, however, and according to him the hypocerebral ganglion is present in lamellicorns but absent in some other groups of Coleoptera.

From the close similarity of scolytid and lamellicorn nervous systems we might expect to find a hypocerebral ganglion in the Douglas fir beetle and yet,

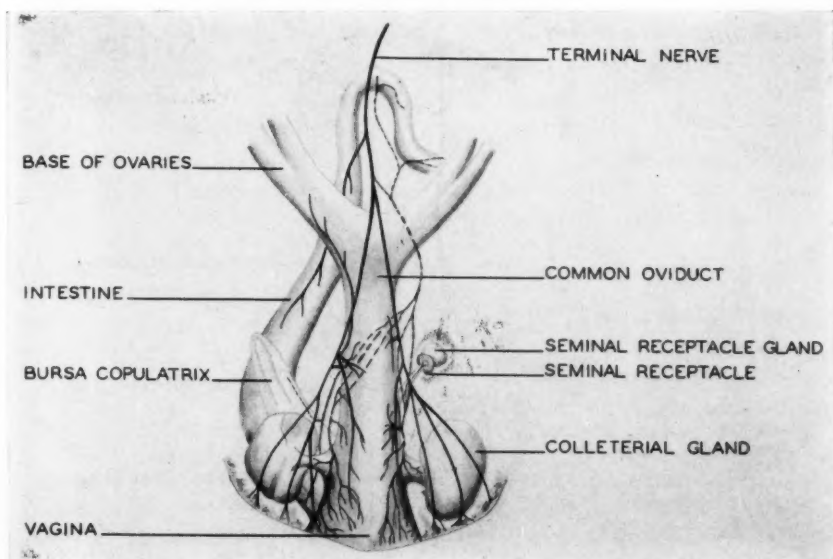


Fig. 5. Female reproductive system and typical nerve supply.

as mentioned previously, there is no swelling along the recurrent nerve. However, the position of the connections between the frontal ganglion and the *C. cardiaca* suggest that possibly the nerve cells which constitute the hypocerebral ganglion of other beetles and insects are located within the frontal ganglion, due to the unusually posterior position of the latter in the Douglas fir beetle. In this respect it is interesting to note that according to Cazal, nerve connections between the recurrent nerve and the *C. cardiaca* are present in some beetles but absent in others. He does not give information on such connections for *Melolontha*.

We have observed only one nerve connecting each *Corpus cardiacum* with the brain but this can be considered as due to fusion of the two nerves which Cazal reports as typical in insects, and no doubt two pathways are distinct within each side of the brain. The arrangement of the *C. cardiaca* and *C. allata* corresponds with the lateral-distal type of Cazal's four groupings of these structures in insects. It is difficult to distinguish the finer nerves from tracheal branches under the stereoscopic microscope and we believe a final description of the connections of the stomatogastric nervous system and retrocerebral endocrine system in the Douglas fir beetle must await histological studies.

With respect to the abdominal nerves, the typical arrangement in insects is a distinct pair per segment, regardless of the number of separate ganglia. There are eight abdominal segments in *Dendroctonus* (Hopkins, 1909). The variable relation of the 6th nerve to the terminal abdominal nerve is shown in Fig. 3 and it is assumed that the symmetrical nerves ending in the body wall of the posterior abdominal region (see Figs. 5 and 6) represent the 7th and 8th abdominal nerves.

The reproductive organs are supplied by the terminal abdominal nerve as in other Coleoptera. As mentioned previously there are considerable differences between individuals in the way these nerves branch. There is some anastomosis and the connections often vary in position, although the ultimate destination of

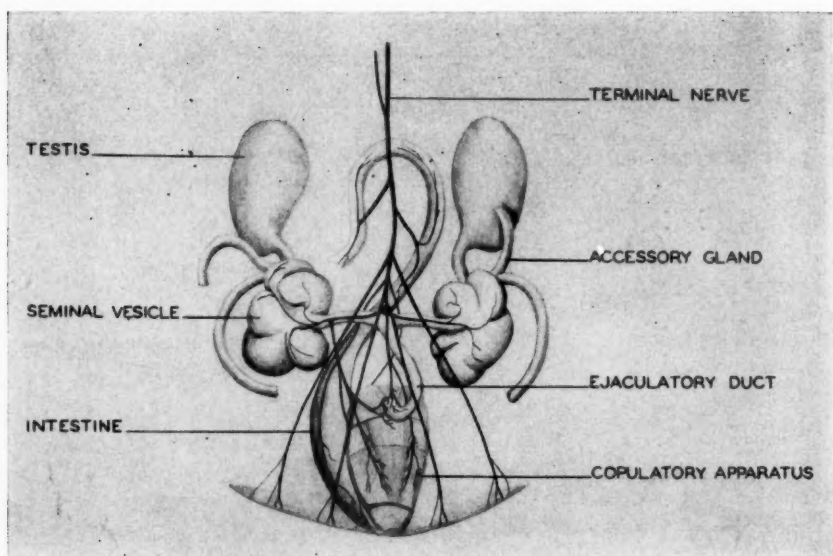


Fig. 6. Male reproductive system and typical nerve supply.

the fibres appears constant. Figs. 5 and 6 therefore represent only what is considered to be fairly typical for the reproductive organ nerves. The only further comment to be made is that a connection from the fourth abdominal nerve to the ovaries or testes, reported by Blanchard to be typical for beetles, was not found.

The drawings and dissections were made by the senior author although the latter were studied by the junior author as well. We thank R. R. Lejeune, Forest Biology Laboratory, Victoria, B.C., for reading the manuscript.

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A Method of Rearing the Pale Western Cutworm, *Agrotis orthogonia* Morr. (Lepidoptera: Phalaenidae), in the Laboratory¹

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Methods of rearing various stages of the pale western cutworm, *Agrotis orthogonia* Morr., in the laboratory have been described (Hocking, 1952; Jacobson, 1952; King and Atkinson, 1927; Lindsay, 1954; Parker *et al.*, 1921; Seamans and McMillan, 1935). From these a very satisfactory method has been evolved at the Lethbridge laboratory that permits this insect to be reared for several generations, providing a source of experimental material at any stage of development. The rearing may be done very satisfactorily at room temperature but, if desired, the method is adaptable to rearing at various conditions of constant temperature and relative humidity.

Eggs may be obtained from two sources: from females collected on flowers in the field during the moth flight (approximately August 15 to September 15) or from adults emerging in the laboratory. Up to 20 males and females, equally divided as to sex, are confined in an animal jar six inches in diameter by eight inches in height. Each jar (Fig. 1) contains soil sifted through a 32-mesh screen to a depth of about half an inch and the cover is fitted with a circular piece of window screen. Food for the moths consists of a solution of one part of honey to 10 parts of distilled water and is contained in a plastic specimen vial one inch in diameter by two inches in height. The top of the vial is cut to allow the insertion of a four-inch piece of lamp wicking and a small capillary tube. The vial containing the honey solution is placed on the surface of the soil in the jar, and access to the food by the moths is provided by a small piece of quarter-inch screening of galvanized wire bent slightly near one end so as to rest on the top of the vial. The honey-water solution is replaced every second day, when the wick and container are thoroughly washed and rinsed. Egg laying commences within two or three days and continues for about 10 days. Each morning the soil is sifted through a 32-mesh sieve and the dead moths and eggs are removed.

The eggs are cleaned of adhering soil particles and debris, and placed in small shell vials. Fourteen to 17 days at a room temperature of about 70°F. or 11 days at 30°C. are required to incubate the eggs, after which they are stored at 0°C. and a relative humidity of 50 per cent until required.

When larvae are needed, eggs are distributed evenly over the surface of moistened blotting paper fitted to the bottom of a petri dish. Hatching commences within a few hours and extends over several days. The larvae are removed with a camel's-hair brush and transferred to 15-x-60 mm. petri dishes, where they are reared to the adult stage. For the first three instars 10 or more larvae may be reared in each dish but for later instars each dish must contain a single larva. The petri dishes with the larvae may be numbered or otherwise identified and stored in trays, which may be labelled with the stage of development or the date of hatching.

For laboratory rearing, one of the most satisfactory and convenient food plants is sprouts of Marquis wheat. The use of wheat sprouts in place of cut sections of leaves as food was first reported by Hocking (1952). A quantity of seed sufficient to fill a 100-cc. beaker is placed in the bottom of a stacking prepar-

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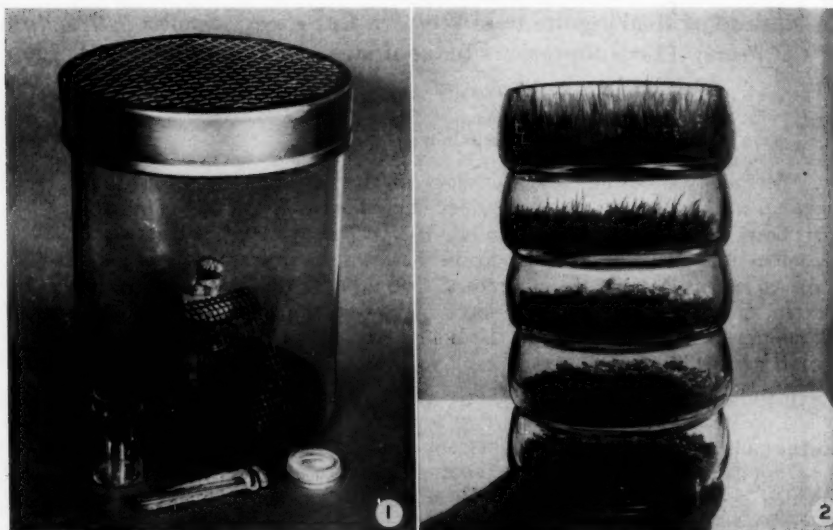


Fig. 1. Animal jar with sifted soil, container for honey solution and screen ladder for moths.

Fig. 2. Stacking dishes with wheat sprouts on five successive days of growth.

ation dish eight inches in diameter by $3\frac{1}{2}$ inches high, and the grain is soaked with water for 24 hours. After the first day when small sprouts are beginning to form, and daily thereafter, the kernels and sprouts are thoroughly washed under a water tap and drained. When grown at room temperature the sprouts are about $1\frac{1}{2}$ inches long on about the fifth day and are ready for use as food. From the first to the third instar, one sprout is sufficient for several larvae but as they grow in size the quantity of food has to be increased. At room temperature new food is added about every second day but at higher temperatures or when uniform larvae are required it is essential that the larvae be fed daily. The method of growing sprouts and stacking the preparation dishes with seed sprouted on successive days is shown in Fig. 2.

The larvae require very little attention, other than feeding, until the fourth instar, when it is necessary to clean the petri dishes of moisture and frass at the time of feeding. This can be done by swabbing the inside of the dish with a one- to two-inch square of blotting paper; or, when the dish becomes completely soiled, it may be replaced with a clean one. The soiled dishes are washed with hot water and soap and dry-sterilized at 150°C . for four hours before being used again.

When the larvae cease feeding they are placed singly in clean containers, where they pupate and emerge. On emergence the moths are identified as to sex and placed in oviposition jars.

At room temperature from 75 to 90 days are required from hatching to emergence but this can be accelerated by rearing at constant temperatures of 25° or 30°C . Survival and vigour of larvae are dependent upon maintaining a constant supply of fresh food. About four hours of daily attention by one person is required to feed and otherwise look after about 500 larvae. This

number is about the minimum to ensure sufficient moths to carry one generation to the next.

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Note on Effect of Flooding on the Carrot Rust Fly in the Holland Marsh Area of Ontario¹

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During hurricane "Hazel", on October 15, 1954, the Holland Marsh, Bradford, Ontario, was flooded with water to an average depth of about four feet. Some sections were covered by more than 10 feet of water and remained flooded for two to three weeks. Data from population studies on the carrot rust fly, *Psila rosae* (F.), conducted in the area by Miss J. B. Williams of the Ottawa laboratory from 1951 to 1953 and by the author in 1954 and 1955 provided an opportunity to determine whether the flood had affected the abundance of the insect.

The Holland Marsh is about 50 miles north of Toronto and covers an area of about 20,000 acres. It is part of the valley of the Holland and Schomberg rivers, which flow into the southern tip of Lake Simcoe. The land on which this study was conducted is the largest section under cultivation and is below the natural water level. It is bounded by 17½ miles of canals, dike embankments holding back the water. A complete description of the Marsh is given by Brownell and Scott (1949).

In Ontario, there are usually two generations of the carrot rust fly each year and the insect overwinters in the pupal stage (Salkeld, 1955). First-generation larvae damage early carrot crops; and second-generation larvae, late carrots. When the Marsh was flooded, most of the flies were in the larval stage of the second generation, although there were some pupae.

The methods of observing and estimating the 1955 population were the same as those of preceding years. Adult emergence was recorded daily by inspecting cages beneath which puparia of the overwintered generation were buried. Weekly counts of adults were made by sweeping in growers' fields of early and late carrots. Counts of larvae and puparia were made semi-weekly in study

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fields of both crops. The latter fields were approximately a twelfth of an acre in size and were divided into 25 plots. Carrot samples taken from each plot were dissected and examined for larvae. Soil samples taken from each plot were sifted through a wire screen and examined for puparia.

Observations in the fall of 1954 and spring of 1955 showed that the flood had killed all of the larvae and most of the puparia. In November, 1954, a post-flood sample of 500 carrots contained 1,028 larvae, all of which were dead. On November 18, 1954, heart action was observed in newly formed puparia taken from a marginal section of the Marsh that had been submerged for about a day. However, flies emerged from only 12 of 41 puparia taken from this location. Puparia from areas that had been submerged for about three weeks showed no signs of heartbeat. In May, 1955, no flies emerged from 300 overwintered puparia dug from the soil of these areas. The mean percentage of adult emergence of the overwintered generation for the previous four years was 54.6.

The numbers of adults captured per 1000 net sweeps and the numbers of larvae and puparia counted per 100 carrots from 1951 to 1955 were as follows:

	1951	1952	1953	1954	1955
Adults per 1000 net sweeps.....	6.1	4.3	27.0	25.3	1.8
Larvae per 100 carrots.....	111.0	59.2	31.1	154.2	0
Puparia per 100 carrots.....	189.7	147.2	152.4	38.6	0

In 1955, the number of adults captured was only 11.5 per cent of the 1951-1954 average. These flies may have emerged from puparia that had overwintered in marginal sections of the flooded area, or, more probably, in adjacent upland farms. Although some flies were present in 1955, no larvae or puparia were found in early or late carrots throughout the Marsh. Possibly the hot, dry weather in 1955 and the extensive use of insecticides in the area were factors that helped to prevent a noticeable infestation. The number of puparia recorded for 1954 was low because the flood occurred when only a small percentage of the larvae had pupated, shortly after the second-generation larval peak.

These results show that prolonged flooding in 1954, by killing the insect in the larval and pupal stages, was largely responsible for the low populations of the insect in 1955.

Acknowledgment

The author is indebted to the Ontario Agricultural College for co-operation in this work.

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North American Subspecies of *Pyrausta unifascialis* (Packard) (Lepidoptera: Pyralidae)¹

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Pyrausta unifascialis (Packard) is the Nearctic representative of a closely knit group which ranges throughout the Holarctic Region and into northern South America, and which includes such species as *P. aerealis* (Hübner), *P. limbo-punctalis* (Herrich-Schäffer), *P. sardinalis* (Guenée), *P. canotinctalis* Hampson, *P. postalbalis* South (= *P. aerealis glauculalis* Caradja, new synonymy), and *P. polygamalis* (Snellen). Study of the considerable series of *P. unifascialis* in the Canadian National Collection shows that four North American subspecies are recognizable, two of them undescribed.

Pyrausta unifascialis subolivalis (Packard)

Figs. 1, 2

Botys unifascialis Packard, 1873: 261.

Botis bircinalis Grote, 1875: 232.

This subspecies is characterized by the extremely uniform dark colouring of the upper surface of both wings and, less constantly, by the infuscation of the under surface of the hind wing. In the male there are only traces of pale markings above; in the female the pale postmedial band and discal spot of the fore wing and the pale postmedial spot of the hind wing are often obvious, but on the average they are far narrower and less contrasting than in the nominate subspecies. The hind wing below is dull creamy, infuscated to a varying degree, sometimes more strongly on the basal than on the distal half, and with the transverse posterior line almost always clearly indicated.

Specimens from the prairies of Canada and from the foothills of the Rockies show a gradual transition to the nominate subspecies, especially in the characters of the hind wing underside. However, the gradient of variation steepens abruptly at the edge of the mountains, and the traditional separation into two subspecies seems justified.

Type localities:—*subolivalis*: Brunswick and Orono, Maine; *bircinalis*: Center, N.Y.

Material examined:—105 specimens, from the following states and provinces: Pennsylvania, New York, Quebec, Ontario, Manitoba, Saskatchewan, and Alberta. Specimens from the Banff and Nordegg regions of Alberta seem best referred to this subspecies, but those from Waterton Lakes Park agree with the following subspecies.

Pyrausta unifascialis unifascialis (Packard)

Figs. 3, 4

Botys unifascialis Packard, 1873: 261.

Botis obnigralis Hulst, 1886: 153.

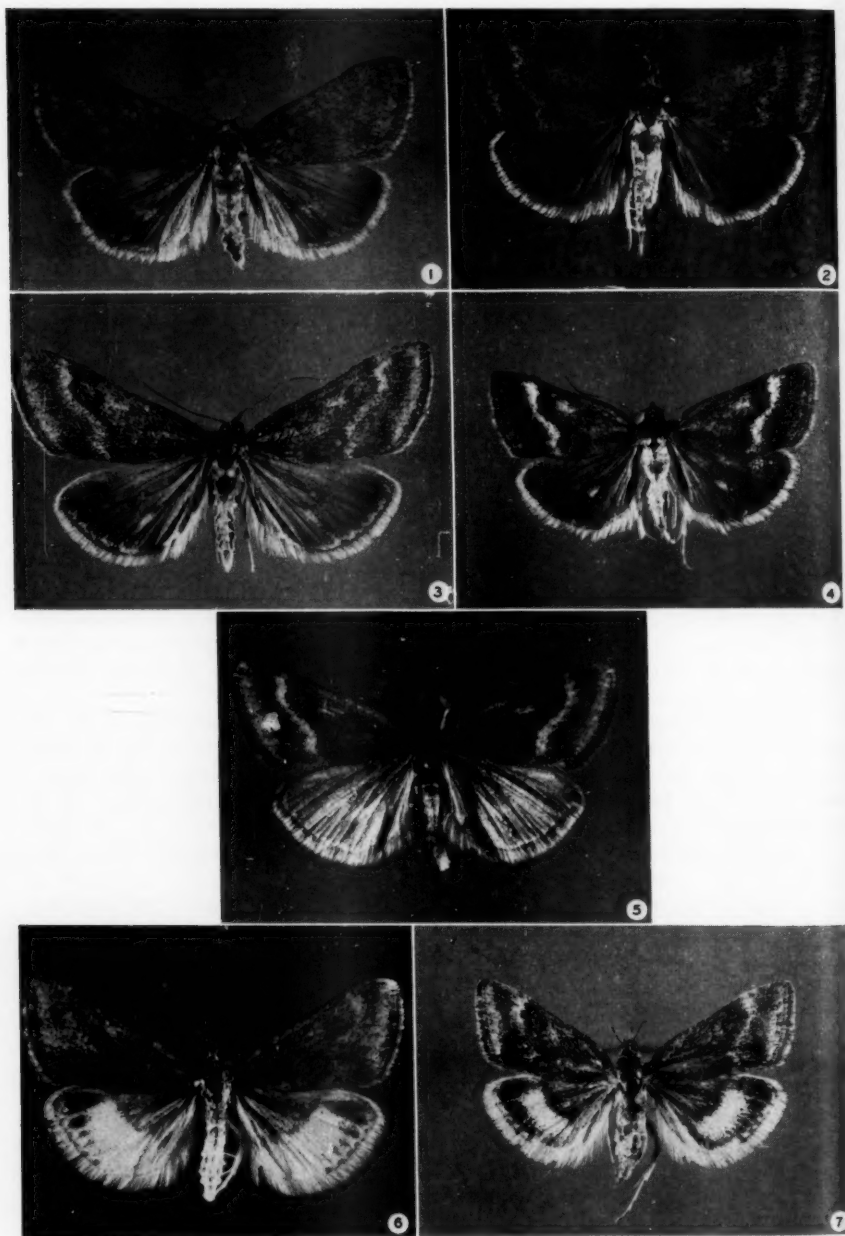
This subspecies differs from *subolivalis* in the greater development of the light markings of the upper surfaces of the wings and in having the under surface of the hind wing whitish and almost immaculate, except for some costal infuscation.

Type localities:—*unifascialis*: California (Edwards); *obnigralis*: Sierra Nevada, California.

Material examined:—181 specimens, from the following states and provinces:

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Figs. 1-7. *Pyrausta unifascialis*: 1, *P. u. subolivacealis*, ♂; 2, *id.*, ♀; 3, *P. u. unifascialis*, ♂; 4, *id.*, ♀; 5, *P. u. arizonensis*, ♂; 6, *P. u. rindgei*, ♂; 7, *id.*, ♀.

Colorado, Wyoming, Montana, Utah, California, Oregon, Washington, Alberta, British Columbia.

***Pyrausta unifascialis arizonensis*, new subspecies**

Fig. 5

Male:—Similar to the nominate subspecies, but with pale markings of fore wing much more prominent; in particular the pale postmedial band broad and complete. Hind wing above without definite pale markings, but often with some pale shading in disc. Fore wing below rather pale, hind wing whitish, overlaid with greenish fuscous.

Female:—Not seen.

The type series is very uniform, and is approached in extent of pale markings on the fore wing only by one or two Wyoming specimens in the extensive material before me.

Holotype, male, Wildcat Creek, White Mts., Ariz., June 12, 1937, Grace H. and John L. Sperry. Paratypes: eight males, same locality and collectors, June 11, 12, and 13, 1937; one male, Kaibab Lodge, Ariz., June 16, 1938, same collectors.

Type No. 6188, C.N.C.

***Pyrausta unifascialis rindgei*, new subspecies**

Figs. 6, 7

Male:—Fore wing almost immaculate above, similar to that of *unifascialis subolivalis*, but on the average paler, because of the lighter shade of the greenish-white powdering. Hind wing above largely white, with a varying degree of fuscous basal and terminal shading. Fore wing beneath dark, with pale powdering on costa and termen, and with indications of a pale postmedial band. Hind wing beneath whitish, immaculate or nearly so.

Female:—Smaller and darker than male; fore wing paler and less distinctly marked than in the nominate subspecies; hind wing dark fuscous, with pale fringe and anal angle and with a large white postmedial fascia. Underside as in the nominate subspecies, but with hind wing uniformly creamy white.

Holotype, male, Rancho La Sierra, near Arlington, Riverside Co., Calif., April 19, 1947, F. H. Rindge. Paratypes:—In the C.N.C.: 18 males, same locality and collector as holotype, various dates in April, May, June, and July; two males, Riverside, Calif., H. Buckwalter, and G. H. and J. L. Sperry; one male, Oak Spring, Riverside, Calif.; four males, San Jacinto Mts., Calif., 5000 ft., F. Grinnell; one male, Gavilan, Calif., G. H. and J. L. Sperry; one male, Upper Santa Ana River, San Bernardino Co., Calif., G. H. and J. L. Sperry; one male, Fish Camp, San Bernardino Mts., Calif., C. Dammers; one male, Mt. Home, Calif., A. L. Melander; one male, Pine Valley, San Diego Co., Calif.; 11 males, three females, Mint Canyon, Los Angeles Co., Calif.

In the Los Angeles County Museum: Allotype, female, and 18 males, three females, Mint Canyon, Los Angeles Co.; two males, two females, San Jacinto Mts., Calif., 5000 ft.; two males, San Bernardino Mts., Calif.; four males, Phelan, Mojave Desert, Calif.; one male, Soledad Canyon, Los Angeles Co., Calif.; one male, Gavilan Hills, Riverside Co., Calif.; one male, San Diego, Calif.

I take pleasure in dedicating this striking subspecies to Dr. F. H. Rindge, who collected a large part of the type series.

Acknowledgments

I am much indebted to Mr. Hugh B. Leech, California Academy of Science, San Francisco, and to Mr. Lloyd M. Martin, Los Angeles County Museum, California, who loaned material that was helpful in this study.

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Spore Coverage and Persistence of *Bacillus cereus* Frankland and Frankland Sprayed on Apple Trees against the Codling Moth¹

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Trials to determine the extent of fruit protection given by spraying spores of *Bacillus cereus* Frankland and Frankland on apple trees exposed to natural attack from the codling moth, *Carpocapsa pomonella* (L.), were carried out in the experimental apple orchard of the Entomology Laboratory at Summerland, British Columbia. Heavy injury was expected there on trees not receiving commercial insecticide applications. Ten test and ten check trees were chosen at random. Check trees received no treatment of any kind. Test trees were treated with six sprays between May 26 and June 29, 1954, and five between August 5 and September 8, 1954.

B. cereus spores were produced by the method of Reed and McKercher (1948) from an inoculum of culture C.M.1-3 (Stephens, 1952) passed eight times through hibernating codling moth larvae, thereby increasing the virulence 50 times. The spore concentrate contained 3.46×10^9 spores per millilitre with 0.5 per cent phenol as a preservative. Two litres of concentrate were diluted with water to a volume of 20 to 25 gallons to give a concentration of 6.09×10^7 to 7.61×10^7 spores per millilitre in the spray. Each test tree received 2 to 2.5 gallons of spray per treatment, applied by a $1\frac{1}{2}$ -horsepower portable sprayer under 300 pounds' pressure.

A count of the number of spores per leaf before and after each spray was determined from a pooled sample of five leaves by the "drop plate" method of Reed and Reed (1948). Thus an estimate was made of the spore deposit and its variation and persistence.

The first spray produced a mean deposit of 2.46×10^7 spores per leaf but the variation in the number of spores between leaves on the same tree was greater than that between trees (pooled standard deviation, 0.41; standard deviation of the mean of the 10 trees, 0.25). This was a result of uneven spray deposit on some leaves.

The mean deposit of *B. cereus* per leaf on the 10 sprayed trees before and after each of the 11 sprays is shown in Table I. The values listed as before sprays 2 to 11 represent the numbers of spores persisting in the intervals between sprays. There was considerable variation in coverage and persistence from one tree to another as shown by the standard deviation of the mean for each treatment.

After the first spray a mean deposit of 2.46×10^7 spores was present per leaf, in comparison with an expected deposit of 6.92×10^7 spores on the basis of an estimated 10,000 leaves per tree. Allowance being made for wind drift and for variation in application and sampling, the mean count was reasonably

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TABLE I
Mean Logs of Numbers of *B. cereus* per Leaf on Check and Sprayed Trees
during the Experimental Period

Spray	Check	Sprayed	Survival on sprayed trees between sprays %	Interval between samplings days	Rainfall in interval inches
1 Before* After***	1.19 ± .37** 0.56 ± .24	0.33 ± .46 7.39 ± .25			
2 Before After	0.35 ± .29	7.18 ± .20 8.31 ± .21	62	6	0.34
3 Before After	1.44 ± .77	— 8.43 ± .49	—	7	0.20
4 Before After	2.48 ± .28	7.41 ± .38 8.82 ± .34	9	9	0.26
5 Before After	3.05 ± .22	8.56 ± .24 9.87 ± .33	55	5	Trace
6 Before After 2 weeks after 3 weeks after 4 weeks after	3.46 ± .27 1.88 ± .68 2.25 ± .23 1.60 ± .67	8.14 ± .25 9.66 ± .41 7.45 ± .25 6.36 ± .33 5.55 ± .23	2 0.6 0.05 0.008	7 14 7 7	0.34 1.18 0.46 0.00
7 Before After	1.40 ± .81	5.12 ± .44 8.23 ± .41	0.003	9	0.09
8 Before After	2.03 ± .91	6.66 ± .39 9.08 ± .32	3	11	0.10
9 Before After	2.73 ± .16	7.33 ± .35 9.04 ± .20	2	7	0.61
10 Before After	2.86 ± .37	7.46 ± .28 8.13 ± .45	3	7	1.01
11 Before After	2.15 ± .45	6.73 ± .25 8.15 ± .23	4	9	0.31

*Immediately before application of spray.

**Standard deviation.

***Immediately after application of spray.

close to the expected deposit. After further treatments the mean counts were progressively much higher than the theoretical maximum and cannot be explained by errors in sampling and counting. Apparently some spores germinated and multiplication of some vegetative rods occurred after the second and later sprays.

During the flight period of the codling moth, sprayed trees had an average deposit of 1×10^8 spores and rods per leaf (mean of all counts made after the first spray except those in the five-week interval between sprays six and seven). On the basis of an estimate of six square inches for the area of an apple leaf, this gives a concentration of 2.7×10^4 spores per square millimetre and this concentration may be assumed to apply also to the apple surface.

B. cereus occurred in small numbers on check trees throughout the trials (Table I). Before the trials, a small natural population of approximately five

spores per leaf was present. The increase in numbers during the trials was probably due to wind drift as some of the check trees were adjacent to test trees.

Scatter diagrams indicated that there was no correlation between the amount of rainfall or the length of interval between sprays and the persistence of spores. It is concluded that the variation in persistence was caused by other factors affecting the viability of the bacteria.

The treatments did not protect the fruit from codling moth damage. The 10 sprayed trees produced 1,685 apples of which 53.7 per cent were wormy, in comparison with 618 apples and 48.2 per cent for the check trees. The habits of the codling moth protect it from bacterial infection. The larva travels only a short distance before entering an apple and hence it can become infected only by ingesting a lethal dose at the point of entry. An average concentration of 2.7×10^4 spores per square millimetre failed to infect a sufficient percentage of larvae to result in fruit protection. (From 74 overwintered larvae collected the following spring from the sprayed trees, there were nine deaths due to *B. cereus*). Application of a higher concentration of spores is economically impractical. Therefore the use of sprays of *B. cereus* shows no promise for control of the codling moth.

Acknowledgments

I wish to thank Dr. J. Marshall, Entomology Laboratory, Summerland, British Columbia, and Mr. J. H. McLeod, formerly of the Entomology Laboratory, Vancouver, British Columbia, now of the Belleville laboratory, for their co-operation and advice in planning and carrying out the field work in this experiment. I also wish to thank Dr. G. E. Bucher, of the Belleville laboratory, for advice during the experiment.

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